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NUMBER 34

PROCEEDINGS
OF
THE 8TH INTERNATIONAL SYMPOSIUM
ON
CHIRONOMIDAE

JACKSONVILLE, FLORIDA

JULY 25-28, 1982

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EDITOR: SELWYN S. ROBACK
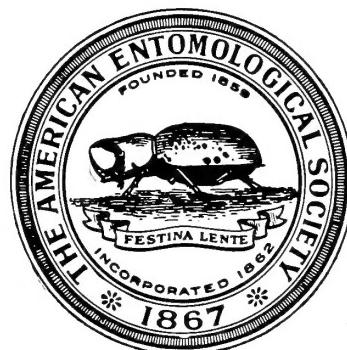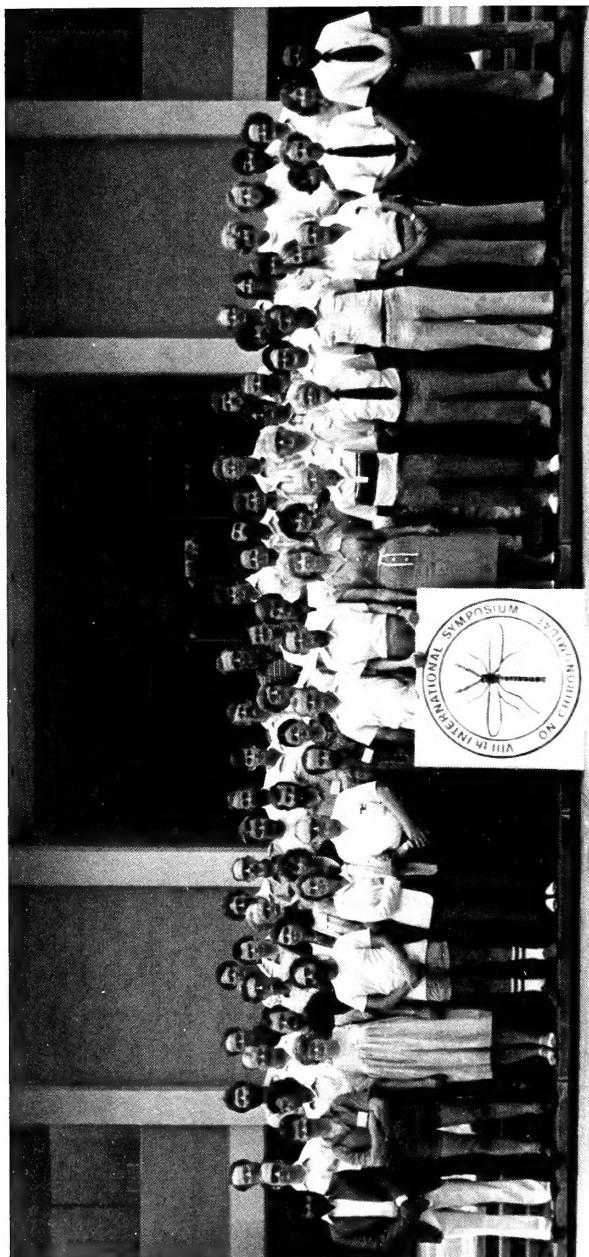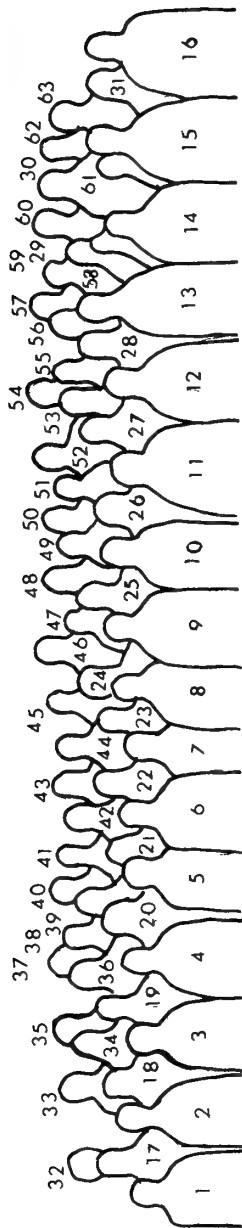
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The 8th International Symposium
on Chironomidae
Jacksonville, Florida, USA, 1982

The 8th International Symposium on Chironomidae was held at Jacksonville University from July 25-28, 1982. The next, in 1985, will be held in Bergen, Norway, hosted by Dr. Ole Saether.

At Jacksonville there were about 65 participants, many accompanied by their wives. Fifteen countries were represented. Thirty-eight papers were given of which 31 plus one from a participant who was unable to attend, are published in these Proceedings. The symposium was followed by an excursion to the Okefenokee swamp, Georgia and Wakulla Springs, Florida.

The Symposium was hosted by Mr. & Mrs. W. Beck, Jr. Thanks are due them, their children and several friends and students who helped with arrangements. Thanks are also due to the officers of Jacksonville University, especially Mr. Richard Lipp and Dr. John Taner, for their hospitality and cooperation. Thanks are also due Dr. D. Webb for editorial help.

<div align="right">Selwyn S. Roback, Editor</div>

Memoirs

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Number 34

Prevalence and Dispersal of Pestiferous Chironomidae
in a Lakefront City of Central Florida, USA

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ABSTRACT. — The prevalence and dispersal of Chironomidae in a lakefront city of Florida was studied. Daily collections of midges from New Jersey light traps placed at the lakefront, and 200 m and 400 m away from the lake were made from January 1980 to December 1981. *Glyptotendipes paripes* Edwards, *Chironomus crassicaudatus* Malloch, and *C. decorus* Johannsen, were quantitatively important. *Glyptotendipes paripes* formed 79.1 and 37.6% and *C. crassicaudatus* 16.7 and 47.1% of the total adults collected in 1980 and 1981, respectively. On some occasions, each of these two species amounted to 100,000 to 350,000 adults per lakefront trap in one night. There was a natural decline of 41% of total chironomids in 1981 compared to 1980. The lakefront traps collected 95-100% of *G. paripes* and 80-100% of *C. crassicaudatus*, in 1980. There was a gradual decline of the two species in relation to the increasing distance from the lake. *Chironomus crassicaudatus* seems to be a stronger flyer than *G. paripes*. It occurred in higher proportions than *G. paripes* in the farther traps from the lake.

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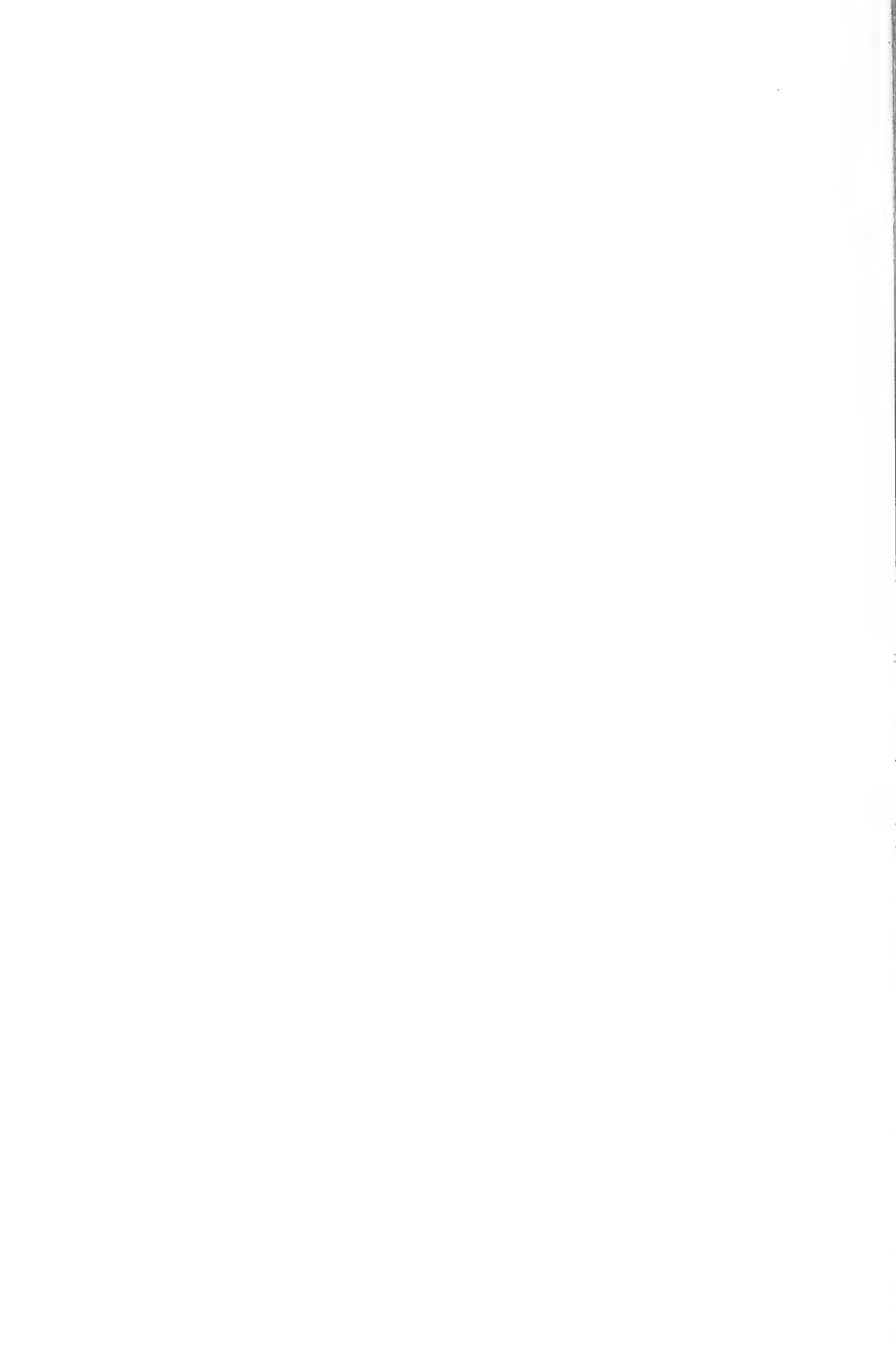
Observations on and Descriptions of the Egg-Mass and Eggs of *Buchonomyia thienemanni* Fitt. (Diptera: Chironomidae).

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ABSTRACT. — The eggs, egg-mass and changes occurring throughout the development of the eggs of *Buchonomyia thienemanni* Fittkau are described and figured. Eggs were studied using the scanning electron microscope (SEM) and the light microscope. The most distinctive feature of the eggs is the presence of a large micropyle at the anterior end which is clearly visible under both the SEM and the light microscope. There are no other apparent pores and the remainder of the egg surface is smooth and structureless. The posterior part of the egg is rounded but the anterior end is slightly tapered and blunt.

The egg-mass is tubular in shape, opaque, yellow in colour and contains approximately 320 eggs packed into the lumen. Development of the eggs from deposition to liberation of the 1st instar larvae takes about five and a half days.

INTRODUCTION

Adults of *Buchonomyia thienemanni* Fittkau were first recorded in Ireland from the River Flesk by Murray (1976) and since then attempts have been made to discover the immature stages. The pupa has recently been described (Murray and Ashe, 1981) but attempts to find the 4th instar larvae of this species in the river after several years searching have not been successful. Dr. H. Tichy (Tübingen) suggested an alternative method of obtaining larvae by first capturing a fertile adult female and then provide suitable conditions for the female to lay eggs from which larvae should hatch. Male adults of *B. thienemanni,* which form distinctly recognisable swarms, were observed during August 1981 near the River Flesk in an attempt to obtain mated pairs falling from the swarm to the ground. On the 9th August a male and female adult of this species were captured in copulo. An egg-mass and eggs were subsequently obtained and are described here in detail. A brief account of the development of the eggs is also given. The 1st instar larvae will be described in a subsequent paper.

MATERIALS AND METHODS

Techniques used to obtain eggs. — A male and female adult of *B. thienemanni* were captured in copulo falling from a swarm adjacent to the River Flesk, Killarney at 7:40 pm on the 9th August 1981. Mating, in the

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end to end position, lasted for 10 minutes. In the laboratory the female was placed in a 9.0 cm diameter petri dish containing river water. The lid of a smaller petri dish (diameter 5 cm) was placed on the water surface within the larger petri dish to provide a dry platform on which the female could rest. The petri dish was then left floating on the surface of water within a large tray in order to avoid major fluctuations in the temperature of the small quantity of water within the petri dish. The female was observed at half-hourly intervals throughout the night and the following day. At night between observations the female was kept in the dark. The female was deliberately placed on the water surface on three occasions during the night, at 9:00 pm shortly after capture, at 1:00 am and at 4:00 am and left on the surface for about two hours in each case in order to encourage it to lay an egg-mass. When on the dry platform the adult female was almost complete-ly inactive except for slight movement of the maxillary palps. On the 10th August at 1:30 pm the female was placed on the water surface to encourage it to lay and at 4:00 pm an egg-mass was laid. Immediately after laying the egg-mass the female became extremely active and flew around inside the petri dish whereas during the entire period since capture little or no activity was observed. The egg-mass was laid under water and attached to the bot-tom of the petri dish.

Rearing the eggs. — The egg-mass was placed in a 9.0 cm diameter petri dish which was half full of river water. This petri dish was then placed float-ing inside a large tray containing water in order to avoid large fluctuations in temperature of the small quantity of water within the petri dish. The temperature of the water in the petri dish varied between 18.5°C and 20.5°C.

On the third day small clusters of an orange coloured fungus developed. Each day thereafter, until the eggs hatched, the egg-mass was placed in a clean petri dish and fresh water was added. This procedure ensured that the fungal colonies did not become very large, although they were clearly evi-dent by the following morning. Very few of the eggs were attacked by the fungus and only a few small colonies of the fungus had begun to grow on the egg-mass by the time most of the eggs had hatched. These precautions were necessary because of the known diverse flora of aquatic Phycomycetes which are parasitic on chironomid eggs causing high or even total mortality in egg-masses depending on the time of infection (Martin, 1981).

SEM Technique. — Non-viable eggs and the larvae were preserved in 75% alcohol. For SEM work the eggs were gradually dehydrated to absolute alcohol. Attempts to clean surface particulate matter from the eggs by sonicating resulted in damage to the specimens so the SEM analysis was based on non-sonicated eggs. The eggs were dried in a Polaron Critical
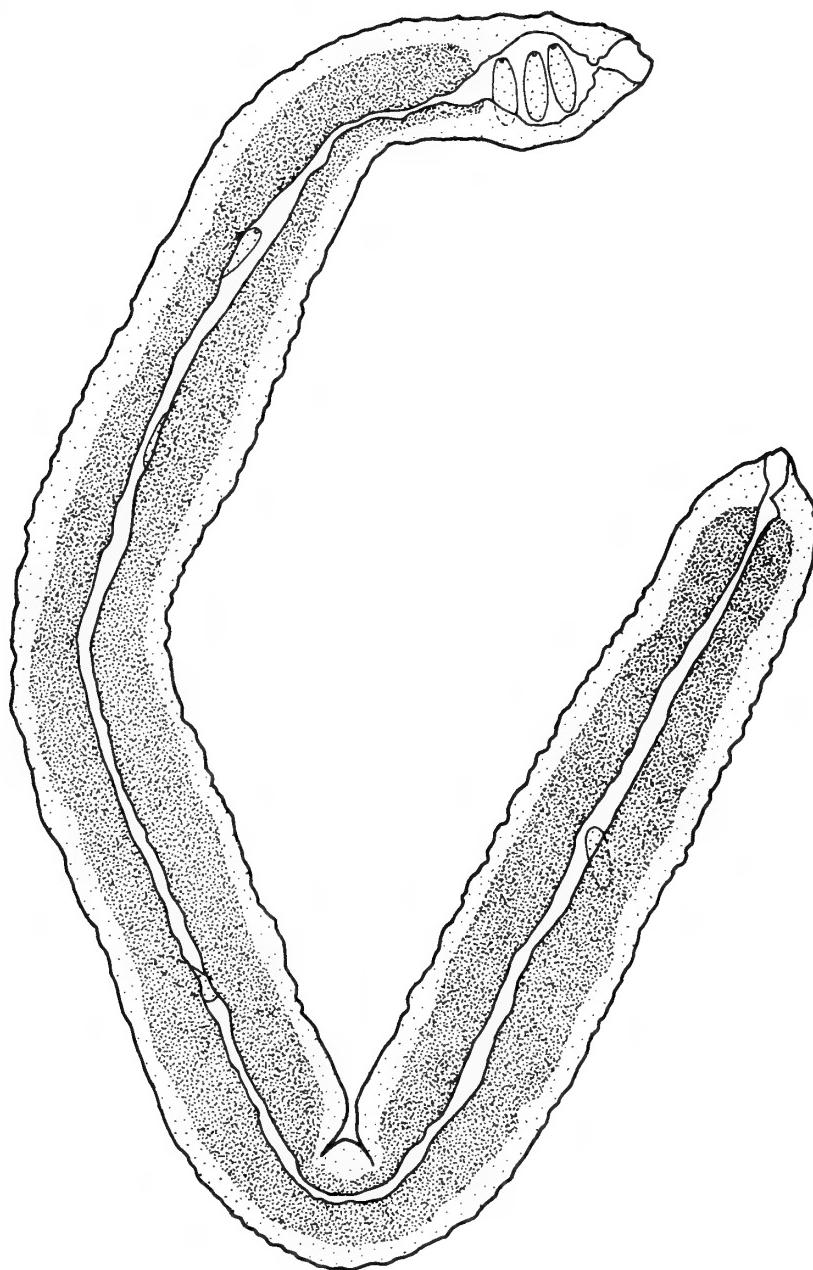
FIG. 1.   Egg-mass of *B. thienemanni* Fittkau.

Point Drier (Model E3000). A stainless steel boat, used to hold a flow-through timble (British-American Optical Company) containing the specimens, was first half filled with absolute alcohol so that the level of alcohol only reaches about half way up the timble. As a consequence of the small size of the eggs the timble was modified in the following way: a piece of teflon tubing with a filter paper at one end was inserted into the timble and a hole made in the timble lid. The eggs were pipetted into the teflon capsule within the timble, the excess alcohol passes through the timble because the porosity of the timble ensures an equal level of alcohol in the boat and timble. The level of alcohol in the boat was lowered so that the eggs, when dried, would be found near the bottom of the capsule. A small disk of filter paper was placed over the top of the teflon capsule to prevent the eggs escaping and the lid of the timble was then secured in position. After drying the eggs were removed from the timble by touching with a fine needle to which they readily adhered. After careful mounting on double sided sticky tape, which was affixed to the top of a stub, the eggs were sputter coated with gold using a Polaron SEM Coating Unit (Model E5100) and examined on a Jeol JSM 35C scanning electron microscope.

OBSERVATONS AND DESCRIPTIONS OF THE EGG-MASS AND EGGS

Description of the egg-mass. — The egg-mass of *B. thienemanni* is approximately 8.9 mm long, roughly tubular in shape and open at both ends (Fig. 1). It is yellow in colour, opaque and the entire surface is very viscous. The eggs are packed into the lumen of the egg-mass. A seam, through which some eggs could be clearly seen, runs along the entire length of the egg-mass. Approximately 320 eggs were contained within the egg-mass (this number was estimated by counting the number of non-viable eggs and the number of larvae that hatched). Of the 320 eggs which were present in the egg-mass 135 or 42% hatched into larvae and 185 or 58% of the eggs were not viable.

Description of the egg. — The eggs of *B. thienemanni* are 230μ long and 92μ wide (widest point). The posterior end of the egg is rounded but the anterior end is slightly tapered and blunt (Fig. 2). The most distinctive feature of the eggs is the presence of a large micropyle, 9.3μ in diameter and 7.0μ deep, at the anterior pole (Figs. 2, 3). There are no other apparent pores and the remainder of the egg surface is structureless and smooth (Fig. 4). The micropyle is clearly visible even under a binocular microscope. Initially, after laying, the eggs are yellow and their contents and the developing larva is clearly visible through the chorion. When the larvae hatch the
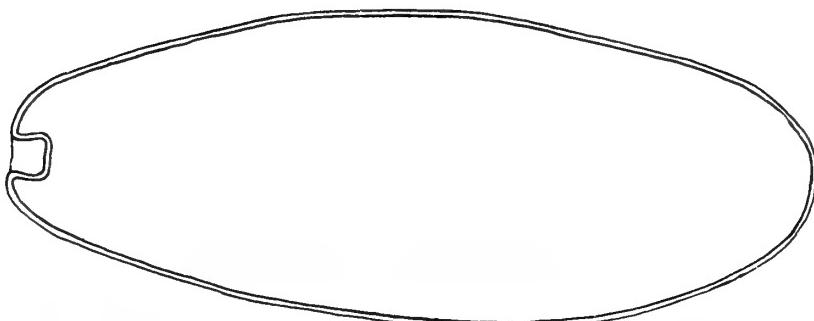
FIG. 2.   Egg of *B. thienemanni* Fittkau.
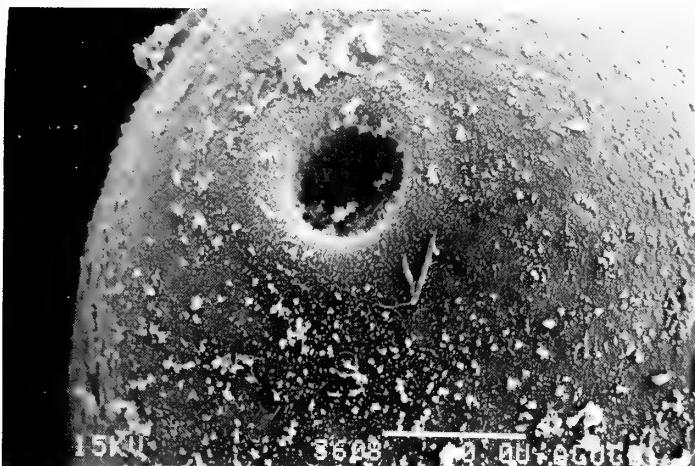
FIG. 3.   Micropyle at the anterior end of the egg of *B. thienemanni* Fittkau.

chorion is clear and colourless. Some particulate matter is present on the surface (Figs. 3, 4) but attempts to clean the eggs by sonicating resulted in damage to the specimens.

Development of the egg. — The development of the eggs of *B. thienemanni* was observed in a field laboratory using a low power binocular microscope which limited the amount of detail that could be seen. The eggs were not observed for more than a few minutes at a time for fear of damage resulting from the heat source in the microscope. Equipment and materials were not available at the time for the proper preparation of the eggs in various stages of development. The drawings of the development are based on sketches
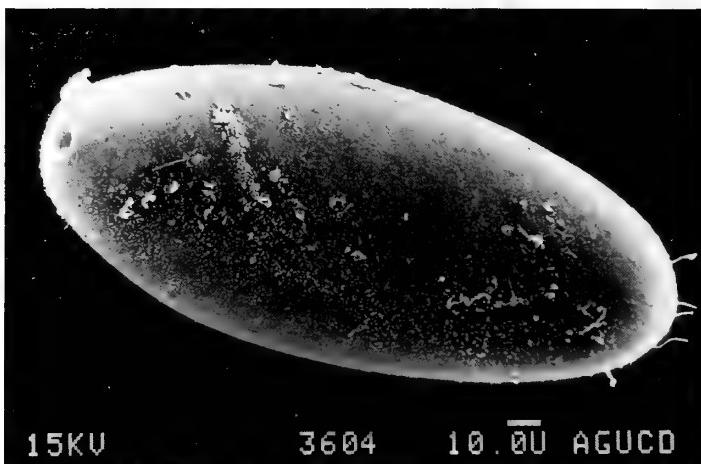
Fɪɢ. 4.   Side view of the egg of *B. thienemanni* Fittkau.

drawn free-hand and the relative size and shape of stuctures may not be exact.

The egg-mass was laid on the 10th August 1981 (Day 1) at 4:00 pm which is regarded as zero hour and the eggs hatched on the 16th August (Day 6) at 10:00 am or 138 hours later. Observations on the eggs are given day by day and the number of hours taken for the eggs to develop to the stages that are described and sketched are indicated.

Day 1.   (0 hour). The embryo at this stage appears undifferentiated and fills the entire space available within the egg (Fig. 5A). (4 hours). The embryo skrinks back from the anterior and posterior ends leaving a clearly defined fluid-filled space at both ends of the egg (Fig. 5B).

Day 2.   (21 hours). The egg has not changed shape but the embryo appears to undergo rapid cell proliferation. The fluid-filled spaces are not as clearly defined (Fig. 5C) as in the previous stage. (29 hours). The dorsal surface of the eggs become slightly concave. A large area of the centre of the embryo becomes quite dense as well as a small area at the anterior end near the micropyle (Fig. 5D). The only space visible within the egg is around the micropyle.

Day 3.   (45 hours). Little visible change is discernible (Fig. 5E) since the previous observation.

Day 4.   (68 hours). The embryo now shows considerable differentiation and about 9-10 lines are visible on the ventral half of the egg which are the first indication of segmentation (Fig. 5F). Fluid-filled spaces are visible at
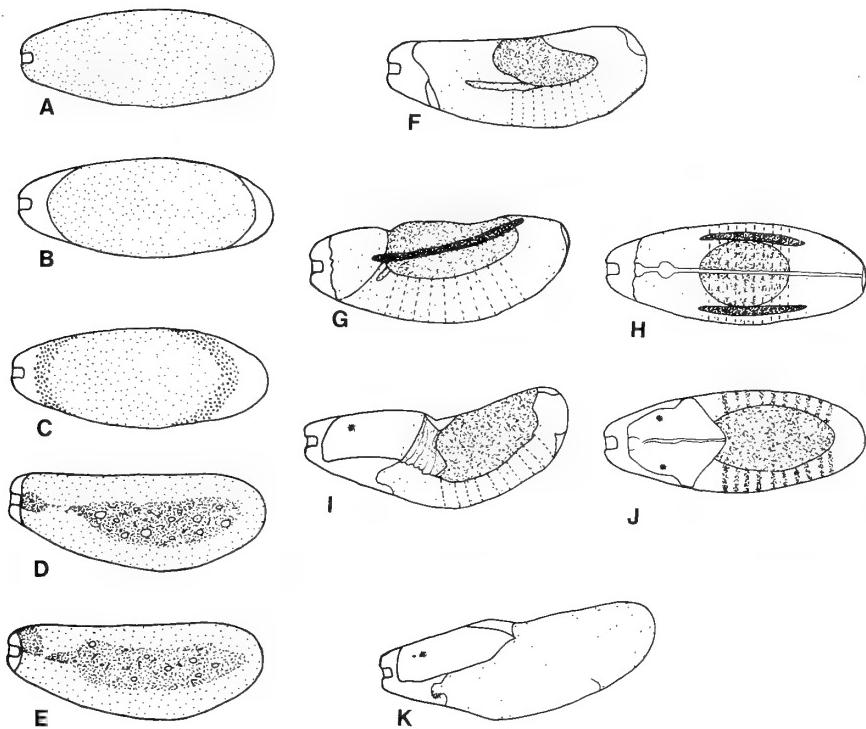
FIG. 5 A-K. Embryonic development in *B. thienemanni* Fittkau: A (0 hours); B (4 hours); C (21 hours); D (29 hours), lateral view; E (45 hours), lateral view; F (68 hours), lateral view; G, H (92 hours), lateral and dorsal view; I, J (116 hours), lateral and dorsal view; K (138 hours), lateral view.

the anterior and posterior ends of the egg. The head region of the embryo is not yet discernible.

Day 5. (92 Hours). In lateral view the head region is clearly distinguished from the rest of the body (Fig. 5G). From the ventral aspect the head region cannot be clearly distinguished from the body although the pharangeal region and the intestine are visible (Fig. 5H). The spaces have decreased in size but are visible at the anterior and posterior ends.

Day 6. (116 hours). The head is much more clearly defined and the eye-spots have developed (Fig. 5I, J). The shape of the eggs in lateral view have changed considerably but if examined in dorsal view they appear not to have changed since Day 1. The pharangeal region is clearly visible but the intestine is no longer visible.

Day 7. (138 hours). When the petri dish containing the egg-mass was ex-
amined some 15 larvae had hatched. The larvae inside the eggs which had
not yet hatched could be clearly seen moving the anterior parapods
backwards against the chorion. Due to the consistency of the abdominal
region and because the larvae were coiled within the eggs it was not possible
to distinguish and draw the structures and segments of this region (Fig. 5K).
Prior to hatching the larvae of *B. thienemanni* begin to swell presumably by
swallowing amniotic fluid. The larvae fill almost the entire egg except for a
few fluid filled spaces at the anterior end.

DISCUSSION

The most detailed and comprehensive study of chironomid eggs and egg-
masses to date is by Munsterhjelm (1920). The egg stage is a very much
neglected part of the life cycle of chironomids and very little information on
even the most basic aspects such as duration of development, hatching
mechanism, embryology, etc. have been published. Most descriptions of
chironomid eggs are very brief and usually little or no information other
than size of the eggs is given. The earliest detailed account of the structure
and development of a chironomid egg is given by Miall and Hammond
(1900) for *Chironomus dorsalis* Auct. Photographs of various stages of
development in the eggs of several species of *Chironomus* are presented in
Strenzke (1950).

The very large and distinct micropyle that is present in *B. thienemanni* is
probably a very plesiomorphic feature and appears to be unique among the
Chironomidae whose egg stage has so far been described. According to
Miall and Hammond (1900) the micropyle in *C. dorsalis* is minute although
its size in relation to the whole egg is not figured. In most descriptions of
chironomid eggs no mention is made regarding the micropyle perhaps
because of difficulties in observing it. Some eggs of *Psectrocladius (Allop-
sectrocladius) obvius* (Walker) were examined in the present study but the
micropyle could not be seen and it may be necessary to examine these eggs
under the SEM.

The most important factor affecting the duration of the egg stage is
temperature. According to Chapman (1975) as temperature increases the
time required for development decreases and conversely as temperature
decreases the time required for development increases in a more or less
linear manner except at the extreme ends of the range for development. In
chironomids this linear relationship between temperature and duration of
development has been demonstrated for the eggs of a *Smittia* species
(Kalthoff, 1971). In *Clunio tsushimensis* Tokunaga the eggs hatch 80-90
hours after oviposition at 25°C (Oka and Hashimoto, 1959) but may take

10-12 days to hatch at 15°C. *B. thienemanni* and *P.(A.) obvius* under similar conditions take about 5.5 and 3.5 days respectively to hatch at a temperature of about 20°C. In *Chironomus plumosus* (Linn.) eggs hatched in 3 days at 24°C and in 14 days at 9° but eggs incubated at 8°C did not hatch and eventually decomposed (Hilsenhoff, 1966). For the majority of chironomids a temperature of between 9-25°C is required for development.

The egg-masses of many chironomid species have been described and it is clear that there is considerable variation in size, shape and form (Munsterhjelm, 1920; Branch, 1928, 1931; Morrow et al, 1968). A key to the egg-masses of some North American chironomid species is given in Morrow et al (1968). The eggs of most species are imbedded in a gelatinous material but the eggs of *Paraclunio* and *Telmatogeton* of the subfamily Telmatogetoninae are laid singly and not in a gelatinous mass (Saunders, 1928; Tokunaga, 1935). According to Hinton (1981) the eggs of *Paraclunio* are inserted into filamentous algae which explains why a gelatinous mass is not produced. In some terrestrial Orthocladiinae the eggs are also laid singly (Hinton, 1981). The egg-mass may contain only one egg or as many as a thousand and within the gelatinous mass specialised structures such as suspensory stalks, anchor chords, etc. may be found (Morrow et al, 1968). According to Hinton (1981) the function of the gelatinous material is to delay desiccation of the eggs when they are exposed above water.

According to Chapman (1975) "Most insects force their way out of the egg, first swallowing the amniotic fluid so as to increase their volume and then pumping blood forwards by contractions of the abdomen so that the head exerts pressure against the shell". The chorion may split in an irregular manner or may split along a line of weakness or cuticular structures, termed egg bursters, usually present on the head, may be used.

The drinking movements observed in *Tanytarsus neoflavellus* Malloch (sub *Calopsectra neoflavellus*) by Davis (1966a, b) probably refer to the uptake of the amniotic fluid as described by Chapman (1975). Before hatching, the larvae of *B. thienemanni* are coiled within the chorion as is the case in *Pseudosmittia gracilis* Goetghebuer (Thienemann and Strenzke, 1940) and in *Chironomus riparius* Meigen (sub *C. thummi thummi* Kieffer) (Strenzke, 1959). In *T. neoflavellus* the larvae are not coiled prior to hatching but lie straight within the chorion (Davis, 1966a). The larvae of *B. thienemanni* were observed moving the anterior parapods backwards and forwards against the chorion which may be an attempt by the larva to weaken the chorion. These movements of the anterior parapods were also noticed in *T. neoflavellus* by Davis (1966a:199) but he apparently did not regard this as being of any importance. Davis (1966a:200) states that the rupture of the egg in *T. neoflavellus* was never accompanied by movement

of the larva and was initiated by internal pressure. Internal pressure alone does not explain why the eggs of *T. neoflavellus* in 59 cases out of 60 burst on the ventral side of the egg just posterior of the anterior papapods. In all cases where larvae of *B. thienemanni* were seen breaking out of the egg the chorion split on the ventral side of the egg close to the anterior parapods. It seems plausible that in *B. thienemanni* and *T. neoflavellus* that the larva weakens the chorion with the anterior parapods and then internal pressure causes the eggs to rupture at this point.

Alternative methods of hatching from the egg by chironomid larvae have been reported. Davis (1966a:201) states that in an unidentified chironomid larva, following a period of drinking movements, the chorion is split dorsally towards the posterior border of the head, above a dark pointed structure which acted as an egg burster. Thienemann (1954) reports that chironomid larvae broke the chorion by using the mandibles.

The description of the egg-mass of *B. thienemanni* given here should readily distinguish it from all other described chironomid egg-masses. The eggs and egg-masses of representatives of the subfamilies Podonominae and Aphroteniinae have apparently not yet been described. The form and construction of the egg-mass in different chironomid subfamilies may be a useful phylogenetic character.

REFERENCES

BRANCH, E.H.   1928.   Description and identification of some chironomid egg masses. Ann. ent. Soc. Am. 21:566-570.
──────────.   1931.   Identification of chironomid egg masses II. Trans. Kans. Acad. Sci. 34:151-157.

CHAPMAN, R.F. 1975. The insects structure and function. The English University Press Ltd. London, 819 pp.

DAVIS, C.C. 1966a. A study of the hatching process in aquatic invertebrates. XVI. Events of eclosion in *Calopsectra neoflavellus* Malloch (Diptera, Tendipedidae). XVII. Hatching in *Argulus megalops* Smith (Crustacea, Branchiura). Hydrobiologia 27:196-207.

——————. 1966b. Hatching processes in the eggs of aquatic invertebrates. Verh. int. Verein. theor. angew. Limnol. 16:1685-1689.

HILSENHOFF, W.L. 1968. The biology of *Chironomus plumosus* (Diptera: Chironomidae) in Lake Winnebago, Wisconsin. Ann. ent. Soc. Am. 59:465-473.

HINTON, H.E. 1981. Biology of insect eggs, Vol. II, 475-778 pp. Pergamon Press Ltd, Oxford.

KALTHOFF, K. 1971. Temperature effects on embryogenesis in *Smittia* spec. (Diptera, Chironomidae): Q_{10}-values of normal development and frequency of "double abdomens" after UV-irradiation. Wilhelm Roux Arch. EntwMech. Org. 168:85-96.

MARTIN, W.W. 1981. *Couchia circumplexa,* a water mold parasitic in midge eggs. Mycologia 73:1143-1157.

MIALL, L.C. AND A.R. HAMMOND. 1900. The structure and life-history of the harlequin fly (*Chironomus*). Clarendon Press, Oxford, 196 pp.

MORROW, J.A., J.L. BATH AND L.D. ANDERSON. 1968. Descriptions and key to egg masses of some aquatic midges in Southern California (Diptera: Chironomidae). Calif. Vector Views 15:99-108.

MUNSTERHJELM, G. 1920. Om Chironomidernas Äggläggning och Äggrupper. Acta Soc. Fauna Flora fenn. 47:1-174.

MURRAY, D.A. 1976. *Buchonomyia thienemanni* Fittkau (Diptera, Chironomidae), a rare and unusual species recorded from Killarney, Ireland. Entomologist's Gaz. 27:179-180.

MURRAY, D.A., AND P. ASHE. 1981. A description of the pupa of *Buchonomyia thienemanni* Fittkau, with notes on its ecology and on the phylogenetic position of the subfamily Buchonomyiinae. Spixiana 4:55-68.

OKA, H. AND H. HASHIMOTO. 1959. Lunare Periodizität in der Fortpflanzung einer spezifischen Art von *Clunio*. Biol. Zbl. 78:545-559.

SAUNDERS, L.G. 1928. Some marine insects of the Pacific coast of Canada. Ann. ent. Soc. Am. 21:521-545.

STRENZKE, K. 1959. Revision der Gattung *Chironomus* Meig. I. Die Imagines von 15 norddeutschen Arten und Unterarten. Arch. Hydrobiol. 56:1-42.

THIENEMANN, A. 1954. *Chironomus.* Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewässer 20:1-834.

THIENEMAN, A. AND K. STRENZKE. 1940. Terrestrische Chironomiden III-IV: Zwei parthenogenetische Formen. Zool. Anz. 132:24-40.

TOKUNAGA, M. 1935. Chironomidae from Japan (Diptera). IV. The early stages of a marine midge, *Telmatogeton japonicus* Tokunaga. Philipp. J. Sci. 57:491-511.

A Biological Appraisal Of Water Quality In The
Ohio River Using Macroinvertebrate Communities,
With Special Emphasis On The Chironomidae

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ABSTRACT. — Macroinvertebrate communities were sampled using multiplate samplers at 15 locations on the Ohio R. and 7 tributary stations in late summer of 1978. The depauperate fauna in the upper Ohio R. pools supports the contention that aquatic habitats subjected to toxic wastes generally possess communities characterized by low numbers of taxa and low densities. In the upper Ohio R. the number of taxa collected per sampling station was inversely correlated with the number of industrial dischargers over the segment of river preceding each of the sampling sites. Interestingly, a mussel survey over the same area in 1979 produced a ranking of the upriver pools in terms of existent mussel species which coincided perfectly with our ranking of numbers of macroinvertebrate taxa collected on multiplates.

Species richness was especially useful in assessing toxic effects, while evenness of distribution of individuals among species was a useful parameter in discerning organic waste input. Chironomid species such as *Cricotopus bicinctus, C. intersectus* gr., and *Dicrotendipes nervosus* Type II were very important in assessing the nature and severity of pollutional impacts. Historically, despite indications of improvement in the Kanawha R., water quality problems apparent in a mid-1960's macroinvertebrate study of the Ohio River Valley still persist.

INTRODUCTION

Early studies of pollutional effects on macroinvertebrate distribution in North America focused on a large-river system (the Illinois R.) (Forbes and Richardson 1913; Richardson 1928). Since that time the majority of North

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American freshwater pollutional work encompassing macroinvertebrate community response has dealt with lake sytems (Carr and Hiltunen 1965; Brinkhurst 1969; Mozley and Howmiller 1977; Saether 1979) or small stream or small river systems. For example, Gaufin and Tarzwell's classical papers (1952, 1955, 1956), using the indicator species concept to assess pollutional impact, had a small midwestern stream (Lytle Creek) as a study site; the use of the highly popular Shannon-Wiener diversity index was developed by Wilhm (1970) and Wilhm and Dorris (1968) from stream or small river work; a third means of pollutional appraisal, the biotic index (Chutter 1972), has been used most extensively in North America by Hilsenhoff (1977). Hilsenhoff's biotic index was developed, and works most effectively, in streams or small rivers possessing a definite riffle component.

The scarcity of large-river pollutional work is due largely to the physical difficulties involved in sampling large rivers and to the inadequate development of taxonomic treatments dealing with large-river macroinvertebrates. Mozley (1979) recently pointed out the lack of information concerning the larval Chironomidae (Diptera) of large rivers. The larval chironomids are an extremely important component of aquatic macroinvertebrate communities; the number of chironomid species often makes up at least 50% of the total macroinvertebrate taxa present in aquatic habitats (Coffman 1978). Fortunately, recent taxonomic treatments of the larval Chironomidae (Oliver et al. 1978; Simpson and Bode 1980) have vastly improved the state of large-river larval chironomid taxonomy. In addition, recent appraisals of pollution in large-river systems using macroinvertebrates collected on artificial substrates (Beckett 1978, Simpson 1980a, b, c, d) have shown promise in elucidating macroinvertebrate response to toxic and organic wastes in large rivers.

This study investigated macroinvertebrate responses to pollutional influences in the Ohio R., a large navigable river in the east-central United States, and some of its principal tributaries in the highly industralized Ohio R. Valley. Results are compared with: 1) fairly extensive chemical sampling performed by the Ohio River Valley Water Sanitation Commission (ORSANCO) over the macroinvertebrate study area; 2) a mussel survey (Taylor 1980) over the upper Ohio R.; 3) a mid 1960's macroinvertebrate study of the Ohio R. (Mason et al. 1971); and 4) other pollutional studies, including Simpson and Bode's (1980) assessment of chironomid response to pollution in large rivers in New York. Questions which are addressed in this study include: will large rivers which are subjected to a complex of pollutional inputs register an interpretable response; and if so, how will this response be expressed at the community and population levels?
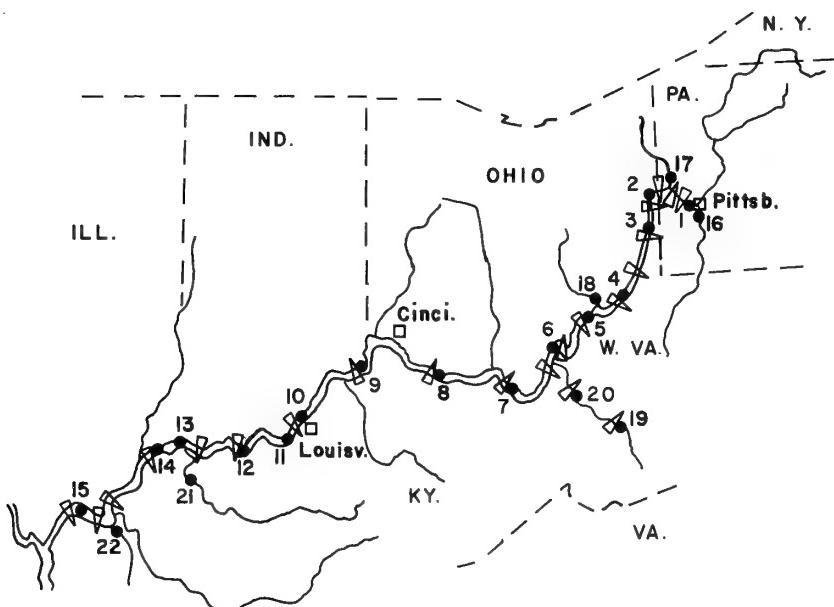
Fig. 1. Map of 1978 Ohio River Valley macroinvertebrate sampling stations. Sampling stations indicated by solid circles; numbers near the circles are station numbers. Triangles indicate the location of dams on the Ohio and Kanawha Rivers while open squares are the large cities of Pittsburgh, Cincinnati, and Louisville.

METHODS

Study Area — The Ohio R. Basin drains a total of 422,170 square km (excluding the Tennessee R. drainage) and includes portions of 11 states. Its primary river, the Ohio, has its origin in Pittsburgh, Pa. at the confluence of the Monogahela and Allegheny Rivers and flows 1578 river km in a southwesterly direction, joining the Mississippi R. at Cairo, Ill. With the exception of the Mississippi, the Ohio R. carries the largest amount of freight of any waterway in the United States — 148 million tons in 1976 (Ohio River Basin Commission 1978). A system of 20 locks and dams over the length of the river maintains a navigational channel for year-around transport. At higher discharges the dams do not impede river flow and the river's current velocity is close to that of natural conditions. At lower flows, however, the dams transform the river into a continuous series of "pools" with current much reduced from natural conditions (United States Army Corps of Engineers 1980). Because of river turbulence thermal stratification
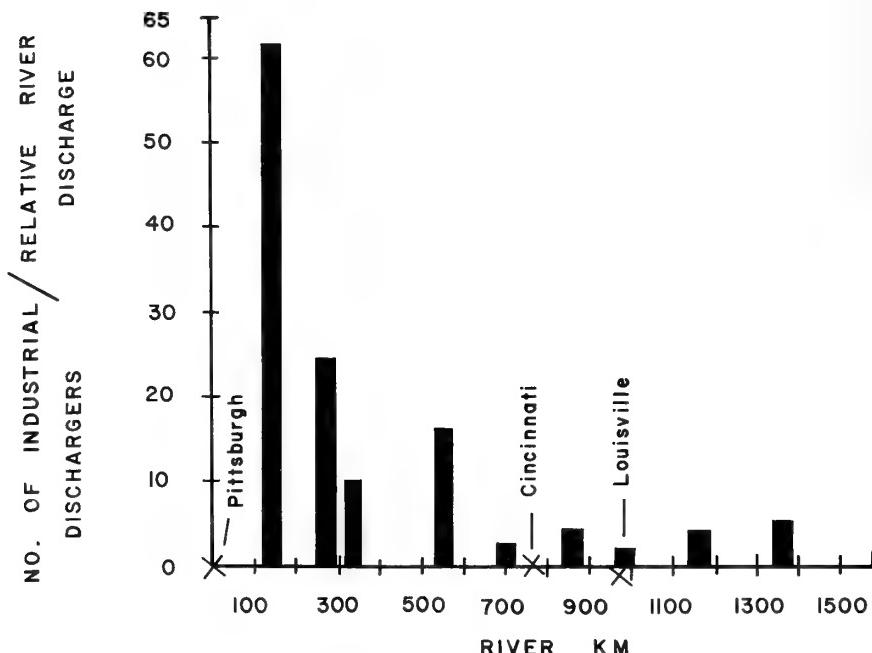
Fig. 2. Number of industrial dischargers per river discharge for segments of the Ohio R. preceding each locks and dam macroinvertebrate sampling site. Segment here is that length of river between sampling sites. Number of dischargers per segment was divided by a "dilution factor" which was equal to the mean river discharge in Sept. 1978 at the respective sampling site (see Table 1) divided by the mean river discharge in Sept. 1978 at the Ohio R. origin (Pittsburgh). The locations of Pittsburgh, Cincinnati, and Louisville are indicated on the abscissa.

does not occur in the river, and water temperatures are identical above and below the dams.

The Ohio R. is subjected to a complex of discharged effluents as a result of its location in the highly industrialized east-central United States. Approximately 200 industrial dischargers release their effluents directly into the Ohio R. Many of these dischargers have multiple discharges. Many other industries (in addition to the 200) send their effluents to municipal sewage treatment plants where the effluents receive primary or secondary treatment and are then released into the river. Approximately 115 municipal sewage treatment plants discharge effluents into the Ohio.

Macroinvertebrate Sampling. — Macroinvertebrate communities were sampled in late summer of 1978 using Hester-Dendy multiplate samplers at 15 locations on the Ohio R. and seven tributary stations (Fig. 1 and Table

1). Artificial substrates are of great utility in comparative pollutional studies since they present a uniform substrate for colonization at each sampling station (United States Environmental Protection Agency 1973; Beak et al. 1973). The multiplate samplers were placed in their respective locations in mid-August and collected in late Sept., giving a six-week colonization period as suggested by the United States Environmental Protection Agency (1973). Samplers were suspended ca. 1 m below the surface. Each sampler consisted of 14 masonite plates separated by a varying number of masonite spacers (spacing varied within the sampler — all samplers were of identical configuration and spacing). Varied spacing was employed since many macroinvertebrates demonstrate a preference for certain microhabitats produced by variable spacings (Mason et al. 1973). Each of the 14 plates per sampler measured 65 mm × 65 mm with a thickness of 3.0 mm.

After collection macroinvertebrate samplers were placed in plastic containers and ethyl alcohol was added as a preservative. In the laboratory samplers were disassembled and the plates "cleaned" of macroinvertebrates with a soft-bristled brush. Macroinvertebrates were amassed by pouring and rinsing the slurry through a U.S. Standard no. 60 sieve. Samples were then stained with rose bengal (Mason and Yevich 1967) to facilitate the sorting of organisms from the organic detritus which had accumulated on the plates. Larval chironomids were prepared for identification using the procedure of Beckett and Lewis (1982).

Three samplers were collected from all sites with the exception of the Ohio R. at Addison (four samplers), the Kanawha R. at London Dam (four samplers) and the Ohio R. at Evansville, Ind. (two samplers). Since species diversity and number of taxa are often dependent on sampling effort (Sanders 1968; Simberloff 1972) three of the four recovered samplers were picked at random at four-sampler sites to report chironomid and total taxa levels, therefore giving a uniform number of three samplers/station. I empirically determined that two samplers had a mean of 80% of the total number of species of three sampler collections. The number of taxa collected at Evansville (two samplers recovered) was therefore adjusted (for both total taxa and number of chironomid species) to an approximate three-sampler level.

Comparisons of number of taxa/station for the Ohio R. sampling sites were done separately for each of the two "types" of sampling stations: those at dams (always located on the upstream, slow-water side of the dam) and those stations not near dams. Beckett and Miller (1982) showed large differences in macroinvertebrate distributions between above-dam and below-dam sites in the Ohio R., thereby necessitating these two separate comparisons.

TABLE 1.   September 1978 Ohio R. Valley macroinvertebrate sampling sites. Discharge data are the mean discharges for Sept. 1978 at the respective sampling locations.

Station	Station No.	River Mile	River Km	Discharge (m³/sec)
O.R.[1] at South Heights, Pa.	1	15.2	24.5	294.5
O.R. near East Liverpool, Oh.	2	43.0	69.2	339.8
O.R. at Pike Island Dam	3	84.2	135.5	351.2
O.R. at Willow Island Dam	4	161.8	260.3	360.0
O.R. at Belleville Dam	5	203.9	328.1	490.0
O.R. at Kyger Cr.	6	260.0	418.3	490.0
O.R. at Greenup Dam	7	341.0	548.7	702.3
O.R. at Meldahl Dam	8	436.2	701.8	784.5
O.R. at Markland Dam	9	531.5	855.2	1005.4
O.R. at McAlpine Dam	10	606.8	976.3	1155.5
O.R. at Mill Cr.	11	625.9	1007.1	1164.0
O.R. at Cannelton Dam	12	720.7	1160.0	1246.1
O.R. at Evansville, Ind.	13	791.5	1273.5	1382.0
O.R. at Uniontown Dam	14	846.0	1361.2	1387.7
O.R. at Joppa, Ill.	15	952.3	1532.2	3260.0
Monongahela R. at Pittsburgh, Pa.	16	4.5*	7.2*	133.1
Beaver R. at Beaver Falls, Pa.	17	5.3*	8.5*	37.7
Muskingum R. near Lock & Dam #2	18	5.8*	9.3*	93.5
Kanawha R. at London Dam	19	82.8*	133.2*	NA
Kanawha R. at Winfield Dam	20	31.1*	50.0*	138.8
Green R. near Seebree, Ky.	21	41.3*	66.5*	104.8
Tennessee R. near Paducah, Ky.	22	6.0*	9.7*	NA

[1]O.R. = Ohio River
* = distance from confluence with Ohio R.
NA = data not available

RESULTS AND DISCUSSION

Macroinvertebrates in the highly industrialized areas of the upper Ohio R. below Pittsburgh and nearby Steubenville and Wheeling are subjected to the effluents of a large number of industrial discharges (Fig. 2). Cyanide and phenolics, both waste products of industrial processes (Hach 1975; ORSANCO 1980), showed proportionately higher percentages of elevated levels in the upriver areas (Fig. 3). Although cyanide and phenolics may not have affected macroinvertebrates directly they served as indicators of industrial effluent impact. In addition, this area of river is near its origin and river discharge is much less than downstream stations (see Table 1), with the river's assimilative capacity thereby lessened.

The depauperate fauna collected at sampling stations 3 and 4 (Fig. 4) supports the contention that aquatic habitats subjected to toxic wastes general-
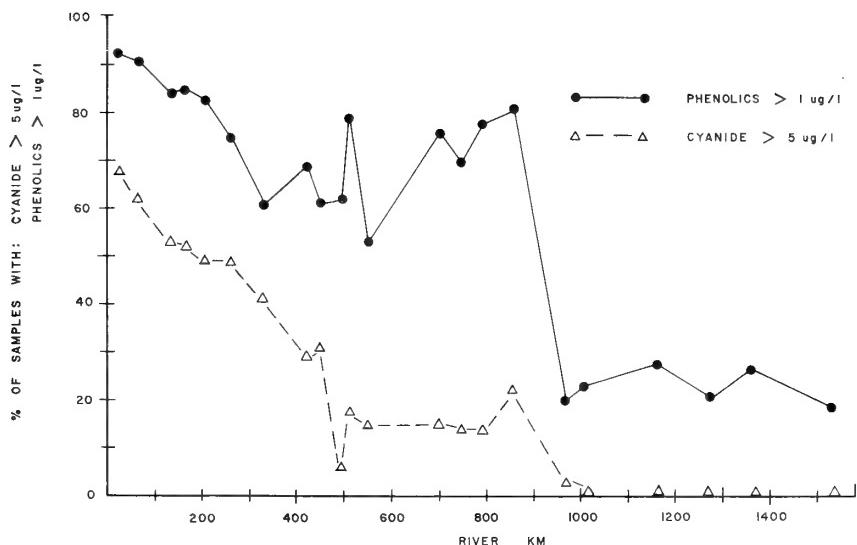
FIG. 3. % of 1978-1979 water samples collected at ORSANCO's Ohio River monitoring stations in which cyanide exceeded levels of 5 μg/1. Also shown is the % of water samples in which phenolics exceeded 1 μg/1. Lines connecting points are for visual continuity and do not indicate percentages at intermediate locations. Data source is ORSANCO (1980).

ly possess communities characterized by low numbers of taxa and low densities (United States Environmental Protection Agency 1973; Hocutt 1975; Lenat et al. 1980). Station 3, the locks and dam sampling station which had the greatest number of industrial dischargers over the preceding segment of the river/river discharge (Fig. 2) (and the highest percentage of elevated cyanide and phenolic levels — Fig. 3) possessed both the fewest total number of taxa and the fewest number of animals per sampler (Fig. 4). Station 4, another upriver station subjected to a relatively large number of dischargers (Fig. 2), also had low numbers of taxa in low densities (Fig. 4). A striking change in the total number of species and number of individuals per sampler was apparent for the macroinvertebrate collection at station 5 vs. those at stations 3 and 4 (Fig. 4). The conspicuous increase in both the total number of species and the number of individuals per sampler at station 5 is probably due to a marked reduction downriver in the number of industrial dischargers (Fig. 2) and the dilution of upstream waters by the addition of water from the Muskingum and Little Kanawha Rivers. Average river discharge for Sept. 1978 increased by only 2% between stations 3 and 4 (Table 1). Discharge increased by 36% between stations 4 and 5, however,
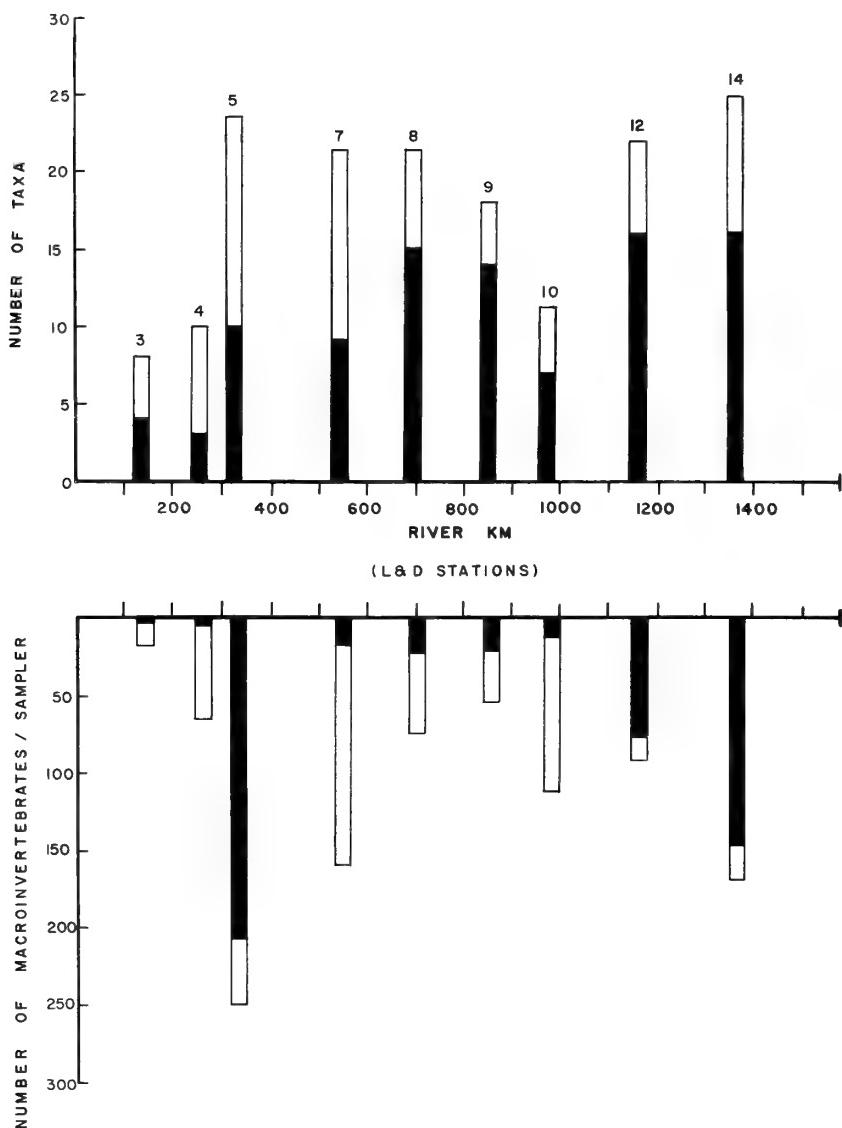
FIG. 4.   Number of taxa/sampling site and mean number of individuals/sampler for Ohio R. locks and dam macroinvertebrate sampling stations. Length of the solid bar denotes the total number of chironomid species collected and the mean number of chironomid individuals per sampler at each site; length of the entire bar denotes the total number of species collected and the mean number of individuals per sampler for all macroinvertebrate taxa at each site. Number above each bar indicates the station number.

due chiefly to the confluence of the two tributaries with the Ohio. The relatively high numbers of taxa and individuals collected at station 5 indicate that toxicity problems have greatly diminished at this point.

A 1979 study of the mussels of the upper Ohio R. (Taylor 1980) presents an interesting comparison with this 1978 macroinvertebrate — artificial substrate study. Although mussels are "macroinvertebrates", they are uncommon on suspended artificial substrates; Taylor therefore studied the same system, over a different year, using a completely different subset of aquatic organisms. He found the Belleville Pool (Belleville Dam is our station 5 — Figs. 1 and 4) "to be the most productive of . . . the pools in total numbers and diversity of [mussel] species" (23 species), while the Greenup Pool (Greenup Dam — our station 7) "had fairly active mussel populations" (14 species). He found the upstream Willow Island Pool (Willow Island Dam — our station 4) to have "only a very scanty mussel population" (3 species), while the Pike Island Pool (Pike Island Dam — our station 3) is "essentially devoid of mussel life" (no species). Taylor's ranking of the upriver pools in terms of number of mussel species present coincides perfectly with our ranking of numbers of macroinvertebrate taxa collected at the upstream sampling sites (see Fig. 4). This shows an encouragingly (scientifically) similar response to environmental conditions has occurred within both communities. Interestingly, the ranking of number of industrial dischargers/river discharge (Fig. 2) is the exact converse of the ranking of the number of macroinvertebrate or mussel species collected, i.e., the upriver sampling station having the highest number of species (station 5 — Fig. 4) had the lowest number of industrial dischargers, the sampling station having the second highest number of taxa (#7) had the second lowest number of dischargers, etc. This inverse correlation suggests that industrial dischargers are exerting a strong influence on macroinvertebrate communities in the upper Ohio.

Downstream sampling stations' total taxa levels did not drop below that of the far upriver stations in either the locks and dam comparison (Fig. 4) or for the non-locks and dam stations (Fig. 5), indicating that the toxicity problems apparent upstream did not recur with such severity for the remainder of the river. The largest numbers of taxa collected on the artificial substrates for both Ohio R. comparisons (Figs. 4 and 5) were at the stations furthest downstream. This is probably due to the reduction in both industrial (Figs. 2 and 3) and organic waste inputs (Fig. 6) and the increased size (and therefore increased assimilative capacity) of the river (Table 1). Water quality of the Ohio R. is also improved by the addition of water from downstream tributaries such as the Green and Tennessee Rivers (Table 3).
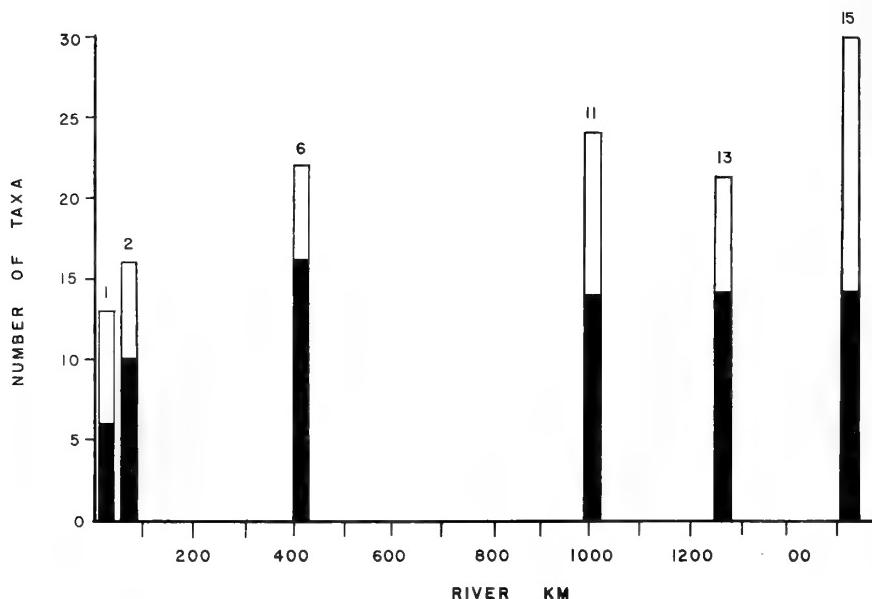
Fig. 5.   Number of macroinvertebrate taxa collected at Ohio R. sampling stations which were not located at dams. Length of the solid bar denotes the total number of chironomid taxa collected at each site while the entire bar refers to the total number of all macroinvertebrates taxa collected per site. Number above each bar indicates the station number.

In addition to industrial inputs, 115 municipal sewage treatment plants discharge organic wastes into the Ohio R. Figure 6 shows that the greatest organic inputs, based on 5-day BODs, are from the large metropolitan areas of Pittsburgh, Cincinnati, and Louisville, with Cincinnati having the greatest impact. Testing for fecal coliforms in 1978-1979 showed that the greatest percentages of high coliform levels occurred below Cincinnati and Louisville (Fig. 7). Causes of the high levels of fecal coliform bacteria include inadequately treated sewage, combined sewer overflows, and urban runoff (ORSANCO 1980). In Sept. 1978 (the month of the macroinvertebrate collections) low dissolved oxygen levels reflected this organic input with dissolved oxygen frequently observed below 5.0 mg/1 from river km 788.4 (just below Cincinnati) to Cannelton Dam at river km 1160 (ca. 200 river km below Louisville) (ORSANCO 1980). The most frequent violations occurred at Markland Dam (station 9 — ca. 100 river km below Cincinnati) at which *Dicrotendipes nervosus* Type II (see Simpson and Bode 1980) was the most abundant chironomid larvae collected (Table 2). Simpson and

Bode (1980) state that "this is often the dominant species in rivers containing both sewage and toxic wastes, and is usually not found in relatively clean waters." In a study of the Great Miami River system (Beckett 1978) *D. nervosus* Type II was almost completely absent from both relatively unpolluted areas and an area in the plume of a chlorinated effluent from a large sewage treatment plant. However, in downstream areas subjected to both toxic and organic wastes *D. nervosus* Type II was the dominant species. The United States Environmental Protection Agency also found this species to be a dominant on artificial substrates placed in the lower Kanawha R. in the late 1960's and early 1970's (P.A. Lewis, personal communication). At that time the lower Kanawha R. was subjected to heavy toxic and organic waste loadings (Mason et al. 1971). The results of these Ohio R. Valley studies therefore agree with those of Simpson and Bode's (1980) in regard to the occurrence of this species.

A comparison of numbers of taxa collected at the various Ohio R. tributary sampling sites (Fig. 8) shows the upstream tributaries near Pittsburgh, the Monongahela and Beaver Rivers, had fewer numbers of taxa collected than the other tributary stations. Macroinvertebrate results from the Beaver R. were of particular interest since this river is degraded by pollution along its entire length (United States Army Corps of Engineers 1980). Table 3 shows that this river had a greater percentage of elevated cyanide and phenolic levels in 1978 and 1979 than even upriver Ohio R. water quality monitoring stations. This tributary supported the lowest number of taxa among the tributary stations sampled (Fig. 8), further supporting the high toxicity — low number of taxa conjecture. Individuals of the species *Cricotopus bicinctus, Nanocladius distinctus,* and *Thienemannimyia* gr. made up 95% of the total number of chironomids (63%, 19%, and 13% respectively) collected at this site. Dominance of the chironomid community by the combination of *C. bicinctus, N. distinctus,* and a species belonging to the *Thienemannimyia* gr. was also apparent in multistressed areas of the Great Miami R. (Beckett 1978). Simpson and Bode (1980) have indicated that these species are prevalent in areas of New York rivers subjected to toxic wastes. *Cricotopus bicinctus* has been found to be abundant in lotic systems receiving electroplating wastes (Surber 1959), chronic stress from copper (Winner et al. 1980), oil contamination (Rosenberg and Wiens 1976), and chlorinated sewage treatment plant effluents (Beckett 1978). Simpson (1980d) found this species to be a dominant in areas of the Niagara R. below industrialized areas. Although *C. bicinctus* is a widespread species and is found both in unpolluted and polluted waters, its tendency to be found as a numerical dominant over a spectrum of toxic conditions makes it a useful indicator of toxic effects.
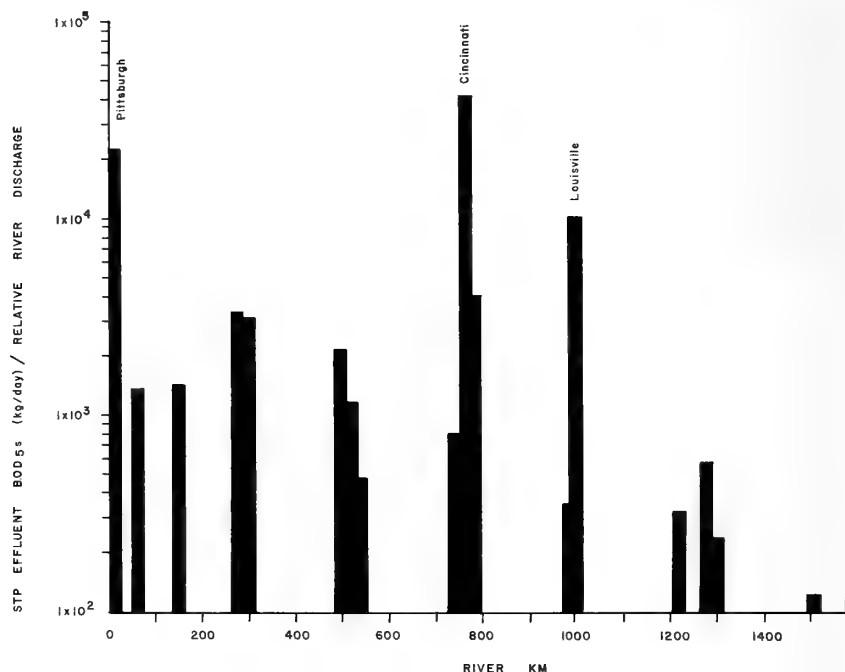
FIG. 6.   5-Day BODs of major (> 1000 kg BOD/day) sewage treatment plant (STP) effluents along the length of the Ohio R. during 1978. At each site BOD input has been divided by the relative river discharge. The relative river discharge is equal to the mean river discharge (Sept. 1978) at that point divided by the mean river discharge in Sept. 1978 at the Ohio R. origin (Pittsburgh) (Table 1). The effluents from the principal STP at Pittsburgh, Cincinnati, and Louisville are indicated. Note that the ordinate is on a logarithmic scale.

The two Kanawha R. sampling stations both supported relatively high numbers of taxa (Fig. 8) but presented an interesting contrast in species composition. *Cricotopus intersectus* gr., averaging 118 individuals/sampler and making up 61% of the chironomid community (Table 2) at Winfield Dam, downstream of Charleston, W. Va., was not represented by even a single individual at London Dam, located 83 km upstream of Winfield Dam. The Charleston sewage treatment plant released an organic-rich effluent in the summer of 1978 (D. Fisher — Dept. of Natural Resources, Charleston, W. Va., personal communication) and daily average dissolved oxygen levels at Winfield were less than 5.0mg/1 for 41.7% of the days in the Sept. 1978 macroinvertebrate sampling period (ORSANCO 1980). Hirvenoja (1973) found *C. intersectus* to be characteristic of eutrophic

TABLE 2. Dominant (by number) taxa at September 1978 Ohio River Valley macroinvertebrate sampling sites. Two most numerous non-chironomid taxa and two most numerous chironomid species shown.

Station No.	Non-chironomid taxa	Chironomids
1	*Gammarus* sp.	*Nanocladius distinctus*
	Nais bretscheri	*Orthocladius* sp.
2	*Dero* sp.	*Nanocladius distinctus*
	Cyrnellus fraternus	*Orthocladius* sp.
3	*Gammarus* sp.	*Cricotopus intersectus* gr.
	Dero sp.	*Nanocladius distinctus*
4	*Cyrnellus fraternus*	*Ablabesmyia parajanta*
	Gammarus sp.	*Nanocladius distinctus*
5	*Cyrnellus fraternus*	*Cricotopus intersectus* gr.
	Potamyia flava	*Polypedilum illinoense*
6	*Gammarus* sp.	*Polypedilum illinoense*
	Cyrnellus fraternus	*Orthocladius* sp.
7	*Stenonema integrum*	*Polypedilum illinoense*
	Gammarus sp.	*Cricotopus intersectus* gr.
8	*Cyrnellus fraternus*	*Dicrotendipes* sp.
	Argia apicalis	*Nanocladius distinctus*
9	*Cyrnellus fraternus*	*Dicrotendipes nervosus II*
	Gammarus sp.	*Polypedilum illinoense*
10	*Cyrnellus fraternus*	*Dicrotendipes* sp.
	Stenonema integrum	*Nanocladius distinctus*
11	*Cyrnellus fraternus*	*Ablabesmyia parajanta*
	Stenonema integrum	*Stenochironomus* sp.
12	*Cyrnellus fraternus*	*Polypedilum illinoense*
	Hydra sp.	*Tribelos* sp.
13	*Cyrnellus fraternus*	*Tribelos* sp.
	Physa sp.	*Dicrotendipes nervosus*
14	*Cyrnellus fraternus*	*Glyptotendipes* sp.
	Stenonema integrum	*Polypedilum illinoense*
15	*Hydropsyche orris*	*Nanocladius distinctus*
	Stenonema integrum	*Parachironomus frequens*
16	*Dugesia tigrina*	*Nanocladius distinctus*
	Dero sp.	*Dicrotendipes* sp. 2
17	*Dero* sp.	*Cricotopus bicinctus*
	Mooreobdella microstoma	*Nanocladius distinctus*
18	*Cyrnellus fraternus*	*Dicrotendipes nervosus*
	Caenis sp.	*Tribelos* sp.
19	*Dugesia tigrina*	*Dicrotendipes neomodestus*
	Gyraulus sp.	*Orthocladius* sp.
20	*Dugesia tigrina*	*Cricotopus intersectus* gr.
	Nais bretscheri	*Orthocladius* sp.
21	*Cyrnellus fraternus*	*Polypedilum illinoense*
	Hydroptila waubesiana	*Dicrotendipes nervosus*
22	*Cyrnellus fraternus*	*Ablabesmyia parajanta*
	Tricorythodes sp.	*Dicrotendipes nervosus*
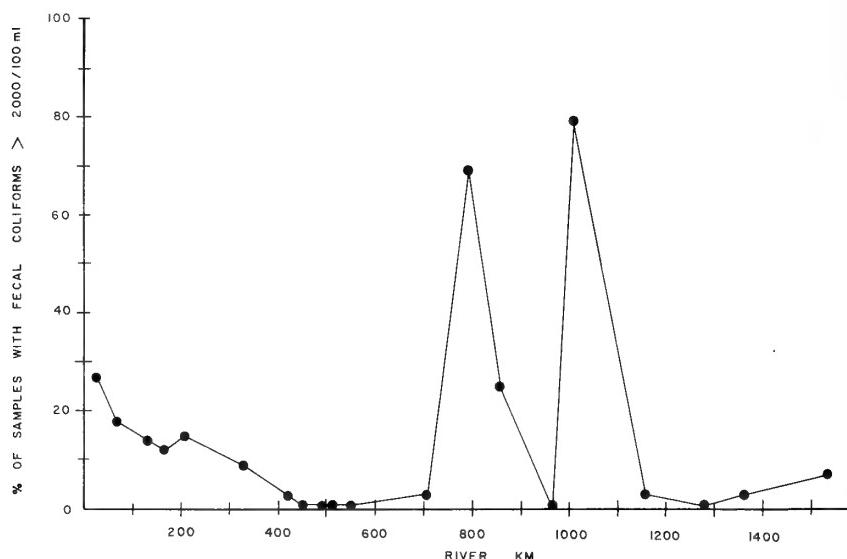
Fig. 7.   % of 1978-1979 water samples collected at ORSANCO's Ohio R. monitoring stations in which fecal coliforms exceeded 2000 counts/100 ml of water. "Peaks" at river km 788 and 1007 are at monitoring stations located a short distance downriver from Cincinnati and Louisville, respectively. Lines connecting points are for visual continuity and do not indicate percentages at intermediate locations. Data source is ORSANCO (1980).

lakes, existing in a wide range of dissolved oxygen concentrations, while Simpson and Bode (1980) often found this species group in sluggish areas of rivers and canals subjected to severe organic and toxic waste loadings. The Kanawha R. results therefore add evidence that this species becomes abundant in slow-water areas subjected to fairly high organic loadings. Interestingly this organic loading did not markedly reduce the total taxa levels (Fig. 8). This suggests that, unlike small streams in which organic wastes tend to reduce the number of species present (Bartsch 1948; Tarzwell and Gaufin 1953; Lenat et al. 1980), moderate organic pollution in large rivers tends to reduce evenness and increase the total number of individuals (as a consequence of domination by species such as *C. intersectus* gr.) rather than decreasing the total number of taxa present.

Although problems with organic loadings were manifested at Winfield Dam, the macroinvertebrate collections indicate that, historically, a considerable improvement in water quality has occurred at this site. In a mid-1960's study Mason et al. (1971) found this area to have "odors of hydrogen sulfide and other chemicals . . . in the area of the locks.
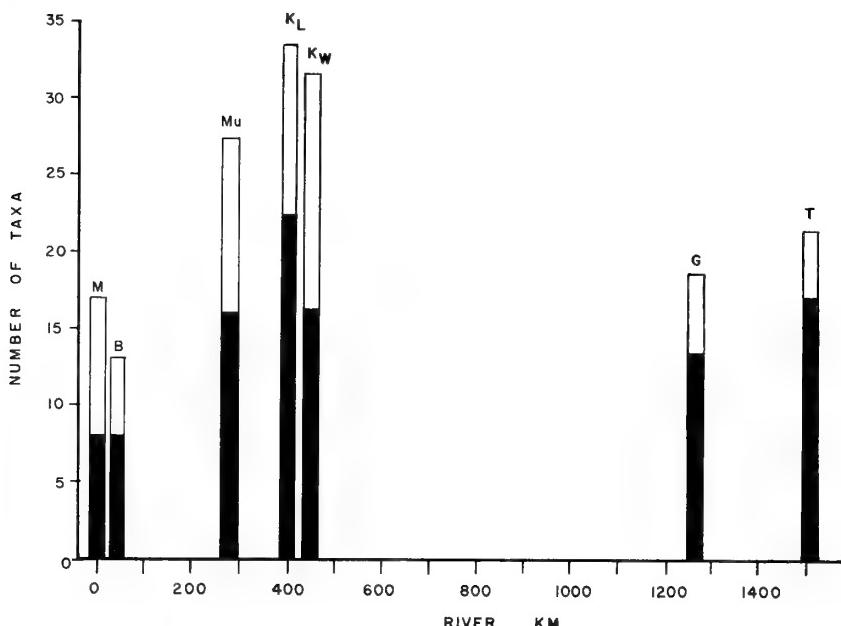
FIG. 8.   Number of macroinvertebrate taxa collected at tributary sampling stations. The solid bar indicates the total number of chironomid taxa collected per site while the entire bar refers to the total number of all macroinvertebrate taxa collected. M = Monongahela R., B = Beaver R., Mu = Muskingum R., K_L = Kanawha R. at London Dam, K_W = Kanawha R. at Winfield Dam, G = Green R., T = Tennessee R. The rivers are placed along the abscissa at their points of confluence with the Ohio R.

Undecomposed leaves, coal fines, and tar-like deposits covered the bottom'' (*D. nervosus* Type II was the most abundant chironomid collected at this site at that time, as mentioned earlier in this paper). Mason et al. (1971) concluded that their artificial substrate samplers (barbecue baskets) "contained mostly worms" and that "low dissolved oxygen concentrations and toxic substances in the water below Charleston greatly reduced the variety of macroinvertebrates."

Despite indications of water quality improvement in area such as the Kanawha R. near Winfield Dam, this study and that of Taylor's (1980) indicate that water quality problems evident in the mid-1960's study (Mason et al. 1971) of the Ohio R. Valley still persist. Mason et al. (1971) summarized their long term study by stating that "macroinvertebrate populations in the industrialized upper Ohio River area were sparse throughout the years sampled. The fauna was characterized by pollution tolerant and

TABLE 3.   Percentages of elevated phenolic, cyanide, and coliform levels for 1978 and 1979 at the Ohio River tributary macroinvertebrate sampling stations. Data source is ORSANCO (1980).

Station	Phenolics (%)		Cyanide (%)		Fecal Coliforms (%)
	$>1\ \mu g/1$	$>5\ \mu g/1$	$>5\ \mu g/1$	$>25\ \mu g/1$	$>2000/100$ ml
Monongahela R. at Pittsburgh, Pa.	86	35	89	32	32
Beaver R. at Beaver Falls, Pa.	88	51	79	22	34
Muskingum R. near Lock and Dam #2	79	21	03	02	12
Kanawha R. at Winfield Dam	61	18	03	00	08
Green R. near Seebree, Ky.	03	00	00	00	07
Tennessee R. near Paducah, Ky.	24	00	00	00	00

facultative organisms. There was a noticeable increase in the number and variety of benthic organisms in the middle and lower reaches of the Ohio River as compared to the upper reach.'' Such trends are apparent in this 1978 study as well as in the mid-1960's.

This study has shown that, even in a complex, large-river situation, macroinvertebrate communities can exhibit an interpretable response to pollution. In this study, species richness has been very useful in assessing pollutional effects, especially in response to toxic wastes. Evenness of species distribution was a useful parameter in discerning organic waste input, especially when coupled with an "indicator species"such as *C. intersectus* (gr.). Although the indicator species concept has recently received considerable criticism it has been a valuable tool in this study when coupled with community parameters such as species richness and evenness. Chironomid species such as *C. bicinctus, C. intersectus* gr., *D. nervosus* Type II, etc. were very important in assessing the nature and severity of pollutional impacts in this large-river study. Because of their great abundance and great species diversity the Chironomidae should be used extensively in pollutional research and water quality monitoring.

Bamber O'Brien for her exceptional assistance in the laboratory processing of the macroinvertebrates.

LITERATURE CITED

BARTSCH, A.F. 1948. Biological aspects of stream pollution. Sewage Works J. 20:292-302.

BEAK, T.W., T.C. GRIFFING, AND A.G. APPLEBY. 1973. Use of artificial substrate samplers to assess water pollution, p. 227-241. *In* J. Cairns, Jr. and K.L. Dickson [ed.] Biological methods for the assessment of water quality, ASTM STP 528. American Society for Testing and Materials, Philadelphia, Pennsylvania.

BECKETT, D.C. 1978. Ordination of macroinvertebrate communities in a multistressed river system, p. 748-770. *In* J.H. Thorp and J.W. Gibbons [ed.] Energy and environmental stress in aquatic systems. National Technical Information Service, Springfield, Virginia. CONF-771114.

_____ AND P.A. LEWIS. 1982. An efficient procedure for slide mounting of larval chironomids. Trans. Am. Microsc. Soc. 101:96-99.

_____ AND M.C. MILLER. 1982. Macroinvertebrate colonization of multiplate samplers in the Ohio River: the effect of dams. Can. J. Fish. Aquat. Sci. 39:1622-1627.

BRINKHURST, R.O. 1969. Changes in the benthos of Lakes Erie and Ontario. Bull. Buffalo Soc. Nat. Sci. 25:45-65.

CARR, J.F. AND J.K. HILTUNEN. 1965. Changes in the bottom fauna of western Lake Erie from 1930-1961. Limnol. Oceanogr. 10:551-569.

CHUTTER, F.M. 1972. An empirical biotic index of the quality of water in South African streams and rivers. Water Res. 6:19-30.

COFFMAN, W.P. 1978. Chironomidae, p. 345-376. *In* R.W. Merritt and K.W. Cummins [ed.] Aquatic insects of North America. Kendall/Hunt Publishing Co., Dubuque, Iowa.

FORBES, S.A. AND R.E. RICHARDSON. 1913. Studies on the upper Illinois River. Bull. Nat. Hist. Surv. 9:481-574.

GAUFIN, A.R. AND C.M. TARZWELL. 1952. Aquatic invertebrates as indicators of stream pollution. Public Health Rep. 67:57-64.

_____. 1955. Environmental changes in a polluted stream during winter. Am. Midl. Nat. 54:78-88.

_____. 1956. Aquatic macro-invertebrates as indicators of organic pollution in Lytle Creek. Sewage Ind. Wastes 28:906-924.

HACH CHEMICAL COMPANY. 1975. Hach water and wastewater analysis procedure manual. Hach Chemical Co., Ames, Iowa.

HILSENHOFF, W.L. 1977. Use of arthropods to evaluate water quality of streams. Wis. Dep. Nat. Resour. Tech. Bull. 100:1-17.

HIRVENOJA, M. 1973. Revision der Gattung *Cricotopus* van der Wulp and iher Verwandten (Diptera, chironomidae). Ann. Zool. Fennici 10:1-363.

HOCUTT, C.H. 1975. Assessment of a stressed macroinvertebrate community. Water Resour. Bull. 11:820-835.

LENAT, D.R., L.A. SMOCK AND D.L. PENROSE. 1980. Use of benthic macroinvertebrates as indicators of environmental quality, p. 97-112. *In* D.L. Worf [ed.] Biological monitoring for environmental effects. D.C. Heath and Co., Lexington, Massachusetts.

MASON, W.T., JR., P.A. LEWIS AND J.B. ANDERSON. 1971. Macroinvertebrate collections and water quality monitoring in the Ohio River Basin 1963-1967. Water Quality Office, United States Environmental Protection Agency, Cincinnati, Ohio. 52 p.

Mason, W.T., Jr. and P.P. Yevich.   1967.   The use of phloxine B and rose bengal stains to facilitate sorting benthic samples. Trans. Am. Microsc. Soc. 86:221-223.

Mozley, S.C.   1979.   Neglected characters in larval morphology as tools in taxonomy and phylogeny of Chironomidae (Diptera). Entomol. scand. Suppl. 10:27-36.

_____ and R.P. Howmiller.   1977.   Zoobenthos of Lake Michigan. Environmental status of the Lake Michigan region (volume 6). ANSL/ES-40. Argonne National Laboratory, Argonne, Illinois, 148 p.

Ohio River Basin Commission.   1978.   The Ohio River Basin. Ohio River Basin Commission, Cincinnati, Ohio. 66 p.

Oliver, D.R., D. McClymont and M.E. Roussel.   1978.   A key to some larvae of Chironomidae (Diptera) from the Mackenzie and Porcupine River Watersheds. Can. Fish. Mar. Serv. Tech. Rep. No. 791:1-73.

Orsanco.   1980.   Assessment of water quality conditions Ohio River Mainstem 1978-9. Ohio River Valley Water Sanitation Commission, Cincinnati, Ohio. 39 p.

Richardson, R.E.   1928.   The bottom fauna of the Middle Illinois River 1913-1925; its distribution, abundance, valuation, and index value in the study of stream pollution. Bull. Ill. Nat. Hist. Surv. 17:387-475.

Rosenberg, D.M. and A.P. Wiens.   1976.   Community and species responses of Chironomidae (Diptera) to contamination of fresh waters by crude oil and petroleum products, with special reference to the Trail River, Northwest Territories. J. Fish. Res. Board Can. 33:1955-1963.

Saether, O.A.   1979.   Chironomid indicators as water quality indicators. Holarct. Ecol. 2:65-74.

Sanders, H.L.   1968.   Marine benthic diversity: a comparative study. Am. Nat. 102: 243-282.

Simberloff, D.   1972.   Properties of the rarefaction diversity measurement. Am. Nat. 106: 414-418.

Simpson, K.W.   1980a.   Macroinvertebrate survey of the Buffalo River System — 1976. N.Y. State Dep. Health, Environ. Health Rep. No. 8:1-31.

_____.   1980b.   Macroinvertebrate survey of the Allegheny River, New York — 1975. N.Y. State Dep. Health, Environ. Health Rep. No. 9:1-39.

_____.   1980c.   Macroinvertebrate survey of the Mohawk River — Barge Canal System, 1972. N.Y. State Dep. Health, Environ. Health Rep. No. 10:1-43.

_____.   1980d.   Macroinvertebrate survey of the Niagara River — 1976. N.Y. State Dept. Health, Environ. Health Rep. No. 11:1-29.

Simpson, K.W. and R.W. Bode.   1980.   Common larvae of Chironomidae (Diptera) from New York State streams and rivers. N.Y. State Mus. Bull. No. 439:1-105.

Surber, E.W.   1959.   *Cricotopus bicinctus,* a midgefly resistant to electroplating wastes. Trans. Am. Fish. Soc. 88:111-116.

Tarzwell, C.M. and A.R. Gaufin.   1953.   Some important biological effects of pollution often disregarded in stream surveys. Purdue Univ. Engineer. Bull. — Proc. 8th Ind. Waste Conf. 1953:295-316.

Taylor, R.W.   1980.   A survey of the freshwater mussels of the Ohio River from Greenup Locks and Dam to Pittsburgh, Pa. Report to U.S. Army Corps of Engineers, Huntington District, Huntington, West Virginia. 71 p.

United States Army Corps of Engineers.   1980.   Ohio River navigational project operation and maintenance. U.S. Army Corps of Engineers, Cincinnati, Ohio. 229 p.

United States Environmental Protection Agency.   1973.   Biological field and laboratory methods for measuring the quality of surface waters and effluents. United States Environmental Protection Agency, Cincinnati, Ohio.

WILHM, J.L. 1970. Range of diversity index in benthic macroinverterbrate populations. J. Water Pollut. Control Fed. 42:R221-R224.

WILHM, J.L. AND T.C. DORRIS. 1968. Biological parameters of water quality. Bioscience 18:447-481.

WINNER, R.W., M.W. BOESEL AND M.P. FARRELL. 1980. Insect community and structure as an index of heavy-metal pollution in lotic ecosystems. Can. J. Fish. Aquat. Sci. 37:647-655.

A preliminary Study of the Chironomidae (Diptera)
from a Stream in Northern Nigeria

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ABSTRACT. — Male imagines were collected weekly during the dry season, October to June, from a stream below a large reservoir. The stream is perennial and is derived from a piped outlet of hypolimnetic water from the reservoir. The fast flowing, relatively cool water makes this an unusual habitat in the Sudan savanna zone of West Africa.

Forty species were recorded, 19 were new records for Nigeria and 11 were new records for West Africa. A number of cosmopolitan species found throughout Africa were also recorded. *Cricotopus scottae* was the predominant species (69%) and emerged throughout the dry season. *Cladotanytarsus pseudomancus* (6%), *Harnischia curtilamellata* (4%) and *Cricoptus verbekei* (3%) were the next most abundant species in male imagine collections. A preliminary investigation of the distribution of species on the main substrate types is included.

INTRODUCTION

The taxonomy of chironomid male imagines from the Afrotropical region is comparatively well known mainly as a result of the extensive revisions by Freeman (1955, 1956, 1957, 1958). A number of significant contributions have been made since that time for example by Brundin (1966), Dejoux (1968, 1969, 1970a, 1970b), Harrison (1970, 1971, 1978) and Lehmann (1979, 1981). However, despite this, comparatively little is known about the geographical distribution and ecology of chironomids from the region, particularly those associated with lotic habitats. This study is a preliminary investigation of the chironomid fauna from an unusual lotic habitat in northern Nigeria.

STUDY AREA

The stream site is located in the south-west corner of Kano State in northern Nigeria and lies in the Sudan savanna vegetation belt (Fig. 1). The site is below the dam wall of a reservoir, Tiga Lake, which was created in 1974. The climate of the area is characterised by distinct wet and dry seasons (Fig. 2). The wettest months are June, July, and August. No rain falls from November to March. This period is cooler due to the effect of the

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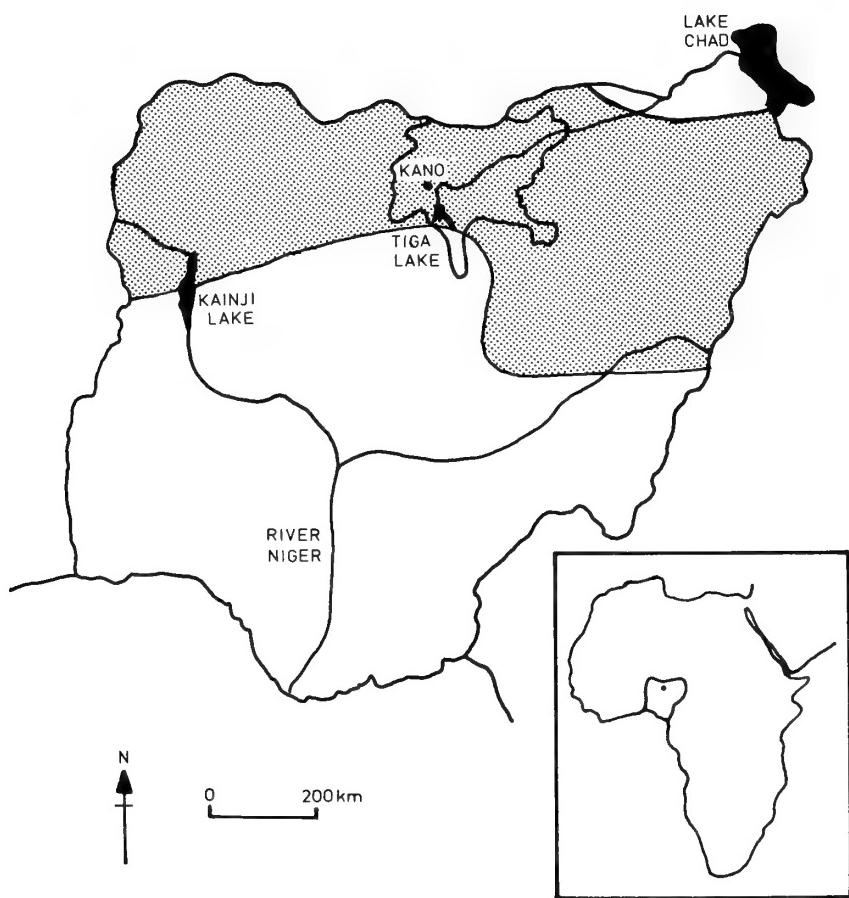
FIG. 1.   Location of stream site in Nigeria. Sudan savanna zone shaded.

Harmattan wind and dust that it carries. The last rain in 1981 was in
September and the first rain in 1982 was at the end of May.

The stream is derived from a piped outlet of hypolimnetic water from the
reservoir. The water is fast flowing and relatively cool. From February to
May 1982 the mean minimum temperature was 20°C and the mean max-
imum temperature was 21.5°C. The temperature of the surface water of
Tiga Lake during this period was 25°C. The stream is perennial whilst
similar natural streams in the area are seasonal. Chemical analysis of the
stream water was carried out on 16-4-82 using Hach DL-EL/4 equipment.
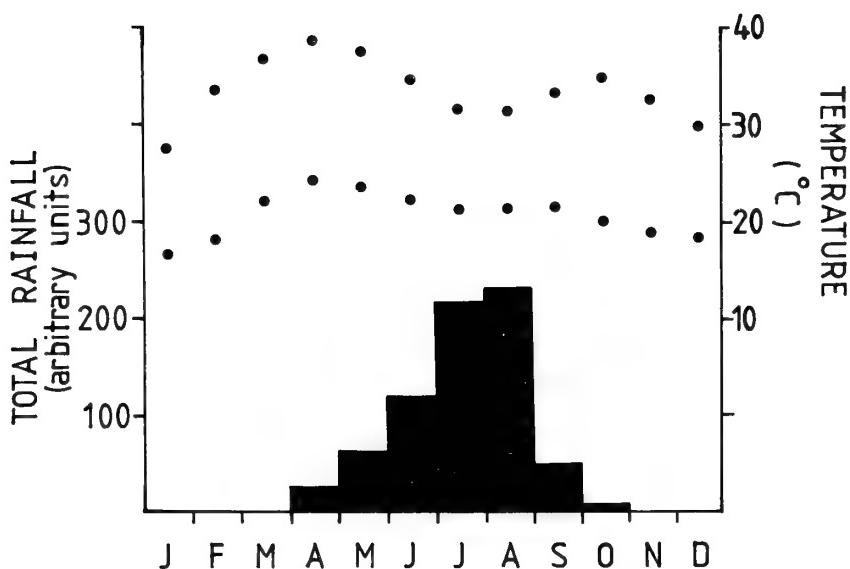
FIG. 2. Climate of the Kano area. Mean maximum and minimum temperatures and rainfall values calculated over a five year period, 1977-1981.

TABLE 1. Chemical characteristics of Tiga stream, 16-4-82. All values in mg l⁻¹ except where given.

Temperature	21°C
pH	8.0
Specific conductance	70 μmhos cm⁻¹
Total alkalinity	40
Total acidity	0
Total hardness	27
Nitrogen, ammonia	0.2
Nitrogen, nitrite	0.015
Nitrogen, nitrate	1.2
Reactive phosphorus	0.26
Dissolved silica	30
Calcium	17
Total iron	0.04
Sulphate	2
Chloride	7

The water is alkaline and contains moderate amounts of nitrogen and phosphorus for this area (Table 1). Silica levels were high due to the sandy soils that predominate.

METHODS

Male imagines were collected from an area of approximately 100m² adjacent to the stream by sweeping vegetation using a fine mesh sweep net. One sample consisted of three 10 minute collections from the area. All collections were made between 9-11 a.m. Twenty-eight samples were collected between September 1981 and May 1982. The mean sampling interval between collections was 8.6 days.

A preliminary investigation of the fauna occurring in different substrates was also carried out. Between November and February two samples, each composed of eight sampling units, were collected from five substrates, marginal vegetation (mainly Gramineae), silt, sand, gravel and stones. The silt, sand and gravel samples were classified using the method described by Salter and Williams (1967). Using their textural triangle the silt substrate should be designated sand as the percentage particle sizes for this sample were 66%, 35%, 4%, 2%, and 3% for coarse, fine and very fine sand, silt and clay respectively. However, the silt and clay proportions were higher than in other samples and the term silt is used here for clarity. Vegetation sampling units consisted of three grass stems cut to approximately 30 cms lengths. Silt, sand and gravel sampling units were collected using a 3 cm diameter plastic corer driven into the sand and closed by hand. Sampling units from the stoney substrate consisted of randomly removed individual large stones. Gravel, sand and silt samples were washed in a 250 μm sieve and larvae were removed from the residue under a binocular microscope. Larvae were removed from vegetation and stones during direct examination under a binocular microscope.

Each of the substrates was also sampled, using the same methods, to provide material for mass rearing. One additional substrate, algae collected from a madicolous habitat, was sampled by scraping algae from 100 cm² of the rock surface. Each substrate sample was placed in a 2.5 1 bucket and covered with stream water. A large glass funnel was inverted and placed over the bucket and an aeration line was inserted through the funnel stem. Imagines were removed from the funnel using a pooter.

RESULTS

As expected, considerable variation in the number of male imagines collected by sweep netting was recorded (Fig. 3). The number of species recorded in each sample also varied throughout the period. However, ignor-
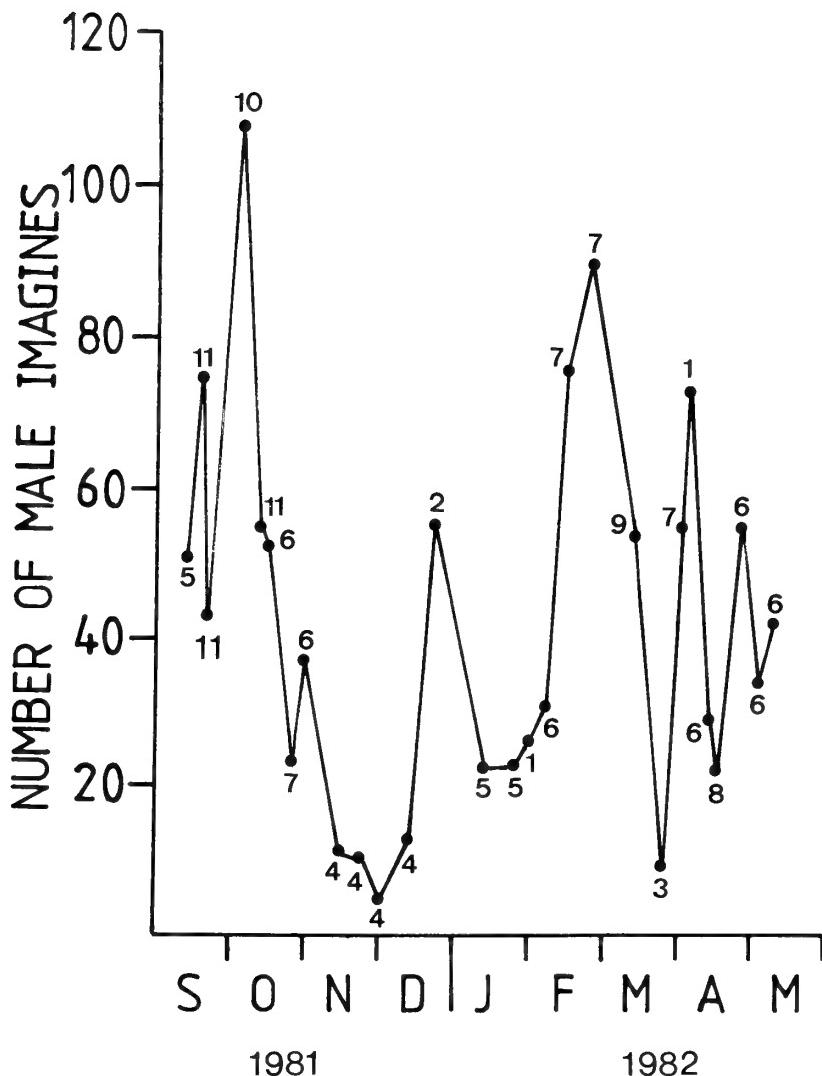
FIG. 3. Variation in the total number of male imagines collected. The number of species recorded is also given.

TABLE 2. Percentage occurrence of species over the period and the months in which they occurred. 1—new for Nigeria, 2—new for W. Africa.

	%	S	O	N	D	J	F	M	A	M
TANYPODINAE										
Pentaneurini										
1. *Conchapelopia cygnus* (Kieffer)	0.2	•	•	•	X	•	•	•	•	•
2. *Larsia rutshuruiensis* (Goetghebuer) 1,2	0.2	•	•	X	•	•	•	•	•	•
3. *Nilotanypus comatus* (Freeman)	0.2	•	•	X	•	•	X	•	•	•
ORTHOCLADIINAE										
Orthocladiini										
4. *Cardiocladius africanus* (Freeman) 1,2	0.3	•	X	X	•	X	•	•	•	•
5. *Cricotopus kisantuensis* (Goetghebuer) 1	1.3	•	•	•	•	•	X	X	X	X
6. *Cricotopus scottae* (Freeman)	69.2	X	X	X	X	X	X	X	X	X
7. *Cricotopus sudanicus* (Freeman)	1.2	•	X	X	X	•	X	X	•	•
8. *Cricotopus verbekei* (Freeman)	2.8	X	X	X	X	X	X	X	X	X
9. *Paraphaenocladius dewulfi* (Goetghebuer) 1,2	2.3	X	X	X	X	X	X	X	X	X
10. *Paratrichocladius* sp. 1,2	2.1	•	•	•	•	X	X	X	•	•
Metriocnemini										
11. *Nanocladius* sp. 1,2	0.1	•	•	•	•	•	X	•	•	•
12. *Pseudosmittia rectilobus* (Freeman) 1,2	1.1	X	X	•	•	•	X	•	X	•
13. *Thienemanniella trivittata* (Goetghebuer) 1,2	0.8	X	•	X	•	•	•	•	•	•
CHIRONOMINAE										
Chironomini										
14. *Cryptochironomus diceras* (Kieffer)	0.7	X	X	•	•	•	•	•	•	•
15. *Cryptochironomus lindneri* (Freeman)	0.1	•	X	•	•	•	•	•	•	•
16. *Cryptochironomus neonilicola* (Freeman) 1	0.2	X	•	•	•	•	•	•	•	•
17. *Cryptochironomus nigrocorporis* (Freeman) 1	0.2	X	•	•	•	•	•	•	•	•
18. *Dicrotendipes kribiicola* (Kieffer) 1	0.1	•	X	•	•	•	•	•	•	•
19. *Dicrotendipes* sp. 1,2	0.6	X	•	•	•	•	•	•	•	•

TABLE 2. Continued

	%	S	O	N	D	J	F	M	A	M
20. *Harnischia curtilamellata* (Malloch)	3.5	X	X	X	X	X	X	X	X	X
21. *Microchironomus stilifer* (Freeman)	1.7	X	X	X	•	•	X	•	•	•
22. *Microchironomus tener* (Kieffer) [1]	0.1	•	X	•	•	•	•	•	•	•
23. *Nilodorum brevibucca* (Kieffer)	0.8	X	X	•	•	•	•	•	•	•
24. *Nilodorum brevipalpis* (Kieffer)	0.2	X	X	•	•	•	•	•	•	•
25. *Nilodosis fusca* (Kieffer)	0.1	X	X	•	•	•	•	•	•	•
26. *Polypedilum abyssiniae* (Kieffer)	0.3	•	•	•	•	•	•	•	•	•
27. *Polypedilum dewulfi* (Goetghebuer)	0.3	•	•	X	X	•	•	•	•	•
28. *Polypedilum kibatiense* (Goetghebuer) [1,2]	0.1	•	X	X	•	•	X	•	•	•
29. *Polypedilum longicrus* (Kieffer)	0.6	•	•	•	•	X	•	•	•	•
30. *Polypedilum melanophilum* (Kieffer)	0.3	•	•	•	X	X	•	•	•	•
31. *Polypedilum pruina* (Freeman)	0.2	•	•	•	•	•	•	•	•	•
32. *Polypedilum* sp. [1,2]	0.1	•	•	•	•	•	•	X	•	•
33. *Xenochironomus trisetosus* (Kieffer) [1]	0.1	•	•	•	•	•	•	X	•	•
34. *Xenochironomus ugandae* (Goetghebuer)	0.1	•	•	•	•	•	•	•	•	X
Tanytarsini										
35. *Cladotanytarsus pseudomancus* (Goetghebuer)	5.6	X	X	•	•	•	•	X	•	X
36. *Cladotanytarsus reductus* (Freeman) [1]	0.4	•	•	•	•	X	X	•	•	•
37. *Rheotanytarsus fuscus* (Freeman) [1,2]	0.2	•	X	X	X	•	•	•	•	•
38. *Tanytarsus pallidulus* (Freeman)	0.3	X	•	•	•	•	•	•	•	•
39. *Tanytarsus spadiceonotatus* (Freeman)	2.0	•	X	X	X	•	•	•	•	•
Unplaced species										
40. *Harnischia* complex sp.	0.1	•	•	•	X	•	•	•	•	•

PERCENTAGE NUMBER
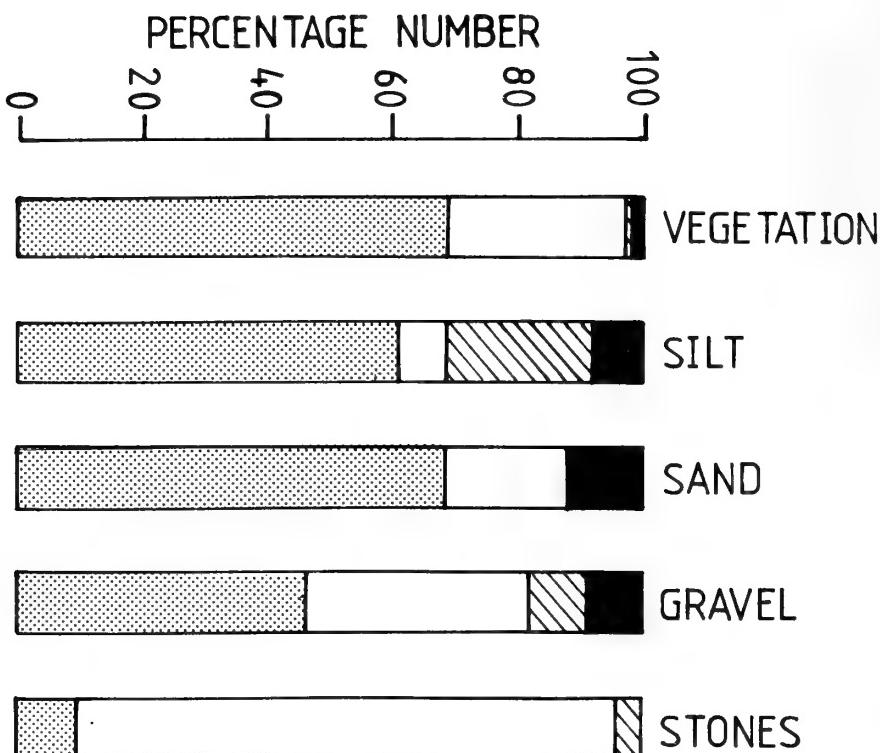
Fig. 4. Proportions of the major taxa recorded in each substrate. Stippled — *Polypedilum,* Clear — *Cricotopus,* Diagonal lines — *Tanytarsini,* Black — others.

ing some of the smaller fluctuations there does appear to be a trend from a large number of species and high numbers in September and October to a low number of species and low numbers in November and December, and then an increase again.

The declining in numbers and species diversity from September was the result of a decline in *Cryptochironomus* species, *Microchironomus* species, *Nildorum* species and *Cladotanytarsus pseudomancus* (Table 2). *C. pseudomancus* did occur later in the study period but only in relatively low numbers.

Larger numbers of Orthocladiinae were recorded than Chironominae. The dominant species throughout the dry season was *Cricotopus scottae* (Table 2). It was recorded on every sampling occasion. *Cricotopus verbekei, Paraphaenocladius dewulfi* and *Harnischia curtilamellata* were recorded every month but not on each sampling date.

· TABLE 3. Species recorded from different substrate types by mass rearing. Species are arranged in order of abundance.

SUBSTRATE	SPECIES
ALGAE (madicolous habitat)	*Larsia rutshuruiensis*
VEGETATION (marginal Gramineae)	*Cricotopus scottae* *Cricotopus verbekei* *Cricotopus sudanicus* *Polypedilum melanophilum* *Rheotanytarsus fuscus* *Polypedilum dewulfi* *Paraphaenocladius dewulfi*
SILT	*Cladotanytarsus pseudomancus* *Cladotanytarsus reductus* *Cricotopus verbekei* *Cricotopus scottae* *Dicrotendipes* sp.
SAND	*Harnischia* complex sp. *Nilotanypus comatus* *Nanocladius* sp.
GRAVEL	*Polypedilum longicrus* *Polypedilum pruina* *Cricotopus verbekei*
STONES	*Cricotpus sudanicus* *Cricotopus verbekei* *Polypedilum dewulfi* *Cardiocladius africanus* *Nilotanypus comatus*

A total of 40 species was recorded from the site (Table 2). 19 species were new records for Nigeria and 11 species were new records for West Africa. Geographical distributions were based on data in Freeman and Cranston (1980).

A preliminary investigation of larval occurrence on five major substrate types was carried out. The upper reaches of Tiga stream drop rapidly producing a turbulent flow of water. Here the substrate is composed of large stones and *Cricotopus* larvae comprised 86% of the chironomid fauna (Fig. 4). As the gradient of the stream decreases the current slows and the substrate changes to gravel, sand and silt, with marginal vegetation composed mainly of grasses. *Polypedilum* and *Cricotopus* larvae occurred in

approximately equal numbers in the gravel substrates (Fig. 4). *Polypedilum* larvae were predominant on vegetation, silt and sand substrates (Fig. 4). Tanytarsini larvae were present in all substrate types, except sand, and were most abundant in silt (Fig. 4).

Mass rearing from each substrate type revealed the actual species composition. Only one species, *Larsia rutshuruiensis*, was reared from algae collected from a madicolous habitat (Table 3). From vegetation only two species of *Polypedilum* were reared and from sand and silt substrates none were reared. *Polypedilum* species were expected in mass rearing from sand and silt substrates on the basis of the larvae collected from these substrates. Three species of *Cricotoptus* predominated the reared adults from vegetation, two species of *Cladotanytarsus* predominated the reared adults from silt and a species belonging to the *Harnischia* complex was the most abundant species from the sand substrate (Table 3). Fewest adults were reared from the sand and gravel substrates.

DISCUSSION

Two streams studied by Lehmann (1979, 1981) in Zaire, central Africa, show a number of similarities with this study. The streams were perennial and showed no major water level or temperature changes throughout the year. The total number of species were comparable although the number of species within each tribe differs (Table 4). The larger number of Chironomini species recorded at the Tiga stream may have been due to collection of imagines that emerged from Tiga lake. This is supported by the fact that several Chironomini species recorded as imagines were not reared from larval material collected from the stream. Comparison with the fauna of the two streams in Zaire suggests that further sampling and rearing may yield a larger species list, particularly for the Orthocladiinae.

Of the seven Orthocladiinae genera recorded from the Tiga stream all but one, *Paraphaenocladius*, were recorded from the river Kalengo by Lehmann (1979). However, the actual species differed. The River Kalengo was dominated by Chironomini, mainly due to *Microtendipes numerosus*, whilst the Tiga stream was dominated by Orthocladiinae, mainly *Cricotopus scottae*. All three streams possessed a number of *Polypedilum* species, several of the same species occurring.

Most species recorded in the River Kalengo by Lehmann (1981) emerged throughout the year. In the Tiga stream *Cricotopus scottae, Cricotopus verbekei* and *Paraphaenocladius dewulfi* were found as imagines throughout the dry season. Several other less abundant species may also emerge throughout the dry season, for example, *Cricotopus kisantuensis* and *Pseudosmittia rectilobus. Cryptochironomus, Microchironomus* and

TABLE 4. Number of species in each tribe. Data for Simisimi stream and the river Kalengo from Lehmann (1979, 1981).

| | NUMBER OF SPECIES | | |
	Tiga stream Nigeria	Simisimi stream Zaire	River Kalengo Zaire
Macropelopiini	0	0	1
Pentaneurini	3	5	6
Orthocladiini	7	13	6
Metriocnemini	3	11	5
Chironomini	22	10	13
Tanytarsini	5	7	7
Total	40	46	38

Nilodorum species were all recorded in September and October immediately after the rainy season but were not recorded subsequently.

Species recorded both in this study and in Zaire by Lehmann (1981) show similar substrate preferences. However, in the Tiga stream considerable overlap was observed in the substrates utilised by species. For example, *Cricotopus verbekei* was reared from substrate samples of silt, gravel, stones and vegetation. Further work is required before any typical species assemblages can be predicted for a particular substrate type.

ACKNOWLEDGEMENTS

REFERENCES

BRUNDIN, L. 1966. Transantarctic relationships and their significance evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. K. Svenska Vetensk Akad. Handl. 11:1-472.

DEJOUX. C. 1968. Contribution a l'etude des premiers etats des Chironomides du Tchad. Hydrobiologie 31:449-464.

_____. 1969. Contribution a l'etude des premiers etats des Chironomides du Tchad (2e note). Description de *Tanypus fuscus* et *Tanypus lacustris*. Bull. Mus. natn. Hist. nat. Paris 41:1152-1163.

_____. 1970a. Contribution a l'etude des premiers etats des Chironomides du Tchad (Insectes, Diptera) (3e note). Description conparee des nymphes de *Chironomus (Nilodorum) brevibucca, Ch. (N.) brevipalpis* et *Ch. (N.) fractilobus.* Bull. Mus. natn. Hist. nat. Paris 42:175-184.

_____. 1970b. Contribution a l'etude des premiers etats des Chironomides du Tchad (4e note). Cah. O.R.S.T.O.M., ser. Hydrobiol. 4:39-59.

FREEMAN, P.   1955.   A study of the Chironomidae (Diptera) of Africa South of the Sahara. Part I. Bull. Br. Mus. nat. Hist. Ent. 4:285-368.
_____.   1956.   A study of the Chironomidae (Diptera) of Africa South of the Sahara. Part II. Bull. Br. Mus. nat. Hist. Ent. 4:285-368.
_____.   1957.   A study of the Chironomidae (Diptera) of Africa South of the Sahara. Part III. Bull. Br. Mus. nat. Hist. Ent. 5:323-426.
_____.   1958.   A study of the Chironomidae (Diptera) of Africa South of the Sahara. Part IV. Bull. Br. Mus. nat. Hist. Ent. 6:261-363.
_____.   AND P.S. CRANSTON.   1980.   Family Chironomidae. In Crosskey, R.W. (ed.) Catalogue of the Diptera of the Afrotropical region. Trust. Brit. Mus. (Nat. Hist.) 175-202.
HARRISON, A.D.   1970.   The Tanypodinae (Chironomidae) of Africa south of the Sahara. Key to known genera and some species. News Lett. Limnol. Soc. South Afr. 15:62-73.
_____.   1971.   A conspectus of the Nacropelopiini and Pentaneurini (Tanypodinae: Chironomidae) of Africa south of the Sahara. Can. Ent. 103:386-390.
_____.   1978. New genera and species of Tanypodinae (Diptera: Chironomidae from Africa south of the Sahara. J. Ent. Soc. 5th. Afr. 41:63-80.
LEHMANN, J.   1979.   Chironomidae (Diptera) aus Fliessegewassern Zentralafrikas (Systematik, Okologie, Verbreitung und Producktionsbiologie) Teil I. Kivu-Gegiet, Ostzaire. Spixiana, Zeitschrift fur Zoologie, Munchen, Suppl. 3:1-143.
_____.   1981.   Chironomidae (Diptera) aus Fliessgewassern Zentralafrikas. Teil II. Die region um Kisangani, Zentralzaire. Spixiana Zeitschrift fur Zoologie, Munchen, Suppl. 5:1-85.
SALTER, P.J. AND J.B. WILLIAMS.   1967.   The influence of texture on the soil moisture characteristics of soils. J. Soil Sci. 18:1-8.

Factors Influencing the Chironomid Community
of a Nearshore Sand Area

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ABSTRACT. — An intensive study of the chironomid fauna in the sandy littoral zone (< 1m depth) of Lough Neagh revealed the important interactions between facies assemblages and community structure. The migratory nearshore bedforms exposed to breaking waves had a more restricted community, both in terms of species and numbers, than their sheltered water counterparts. Some species were more tolerant of sand disturbance than others. These spatial patterns are related to physical factors, for example, wave energy and bottom shear stress.

INTRODUCTION

This small-scale study forms part of a larger survey of the littoral fauna of Lough Neagh. Sand is one of the major littoral habitats (approximately 30% of the shoreline) and a small beach area has been studied since 1980 in order to describe the chironomid community and the life cycles of the species involved. Coincidentally, work has been done on sand bedform movements in the same area. It became apparent that the morphology of the lake bed is an important factor in the distribution of the chironomid community, and this paper attempts to show how different species react to changes in morphology, and to discuss some of the physical factors that cause these changes. An appreciation of these factors is obviously important in the design of a sampling programme for such an area.

STUDY AREA

Traad Beach comprises the northern 100 m of a sandy embayment, Ballyronan Bay, in the north-west corner of Lough Neagh (Fig. 1). The beach opens to the south and is exposed to waves generated by prevailing winds. Waves are generally 0.2 to 0.5 m in height, but may reach over 1.0 m during onshore storms. Wave periods commonly fall between 2 and 4 seconds. Water level in the lake is artifically controlled and varies only a few tens of centimetres over a year. However seiches, set up by winds blowing

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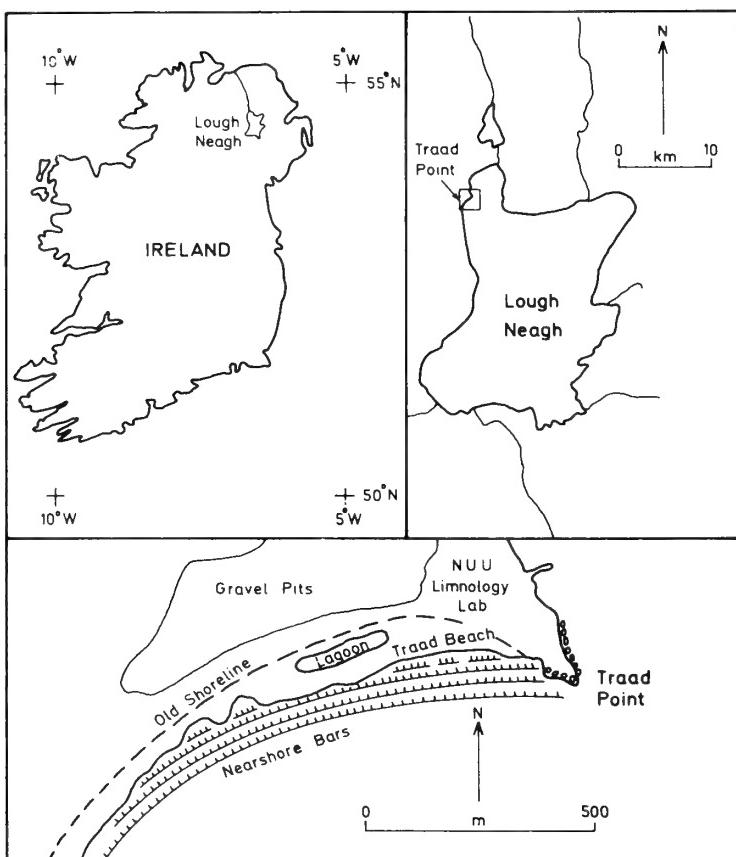
Fig. 1.   Location of the study area.

over the longest fetches (25-30 km) may alter the local water level by 10-15 cm over 30-60 minutes (Carter 1983). The gradient on the nearshore shoaling slope is very low ($< 1°$) and incident waves break into a dissipative, spilling domain. Breaker position is strongly influenced by the position of the nearshore bedforms, consisting of three or four shore-parallel sand bars at depths ranging from 0.1 to 1.2 m. According to wave height, waves break and reform over these bars; energy dissipation due to breaking being between 75-95% of incident wave energy (Carter and Balsillie 1983). The bar bedforms, which have a slow response time relative to wave frequency, show a tendency to migrate landward only during storms or as the lake water level falls. Some of these migrations are quite rapid, up to 0.3m/day,

23 September 1980
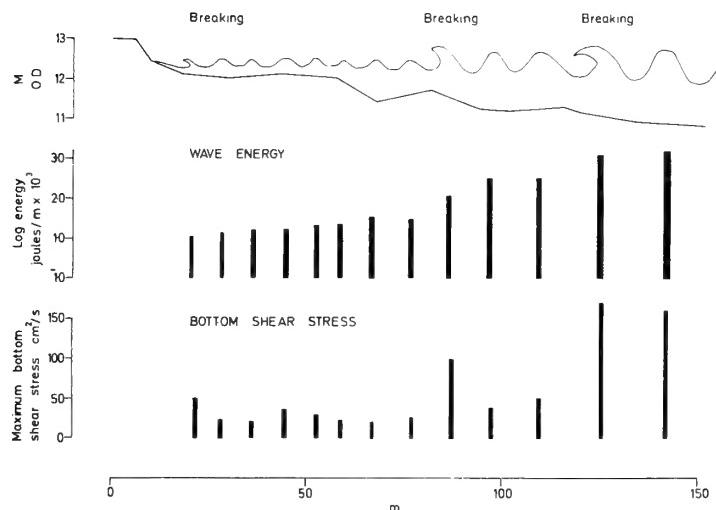
FIG. 2.   Wave energy conditions and bottom shear stress in the study area.

and occur across 10-20 m of the littoral zone. Sediment is returned lakeward by return currents due to wave set-up. The large-scale bedforms are covered by smaller forms — dunes and ripples related to flow regime. Shear stress across the shore increases rapidly around the bar crests, falling away in the bar troughs (Fig. 2).

The beach is bounded by a rocky headland (Traad Point) to the north and a *Phragmites* stand to the south. On the northern side of Traad Point is a gravel shore which changes to sand at a depth of 0.5 m. Some samples were taken from this for comparison.

METHODS

The lake bed was surveyed by Quickset level for the longer profiles, and by measuring the depth below the still water level at regular intervals when the intensive sampling was being done. Sediment cores were taken with a modified Kajak corer and the depth of disturbance of the sand at the sampl-ing points (apparent as a colour difference between the layers of sand) was recorded in the field. In the long term survey, five cores were taken at each site but during the intensive, daily sampling only two cores per site were
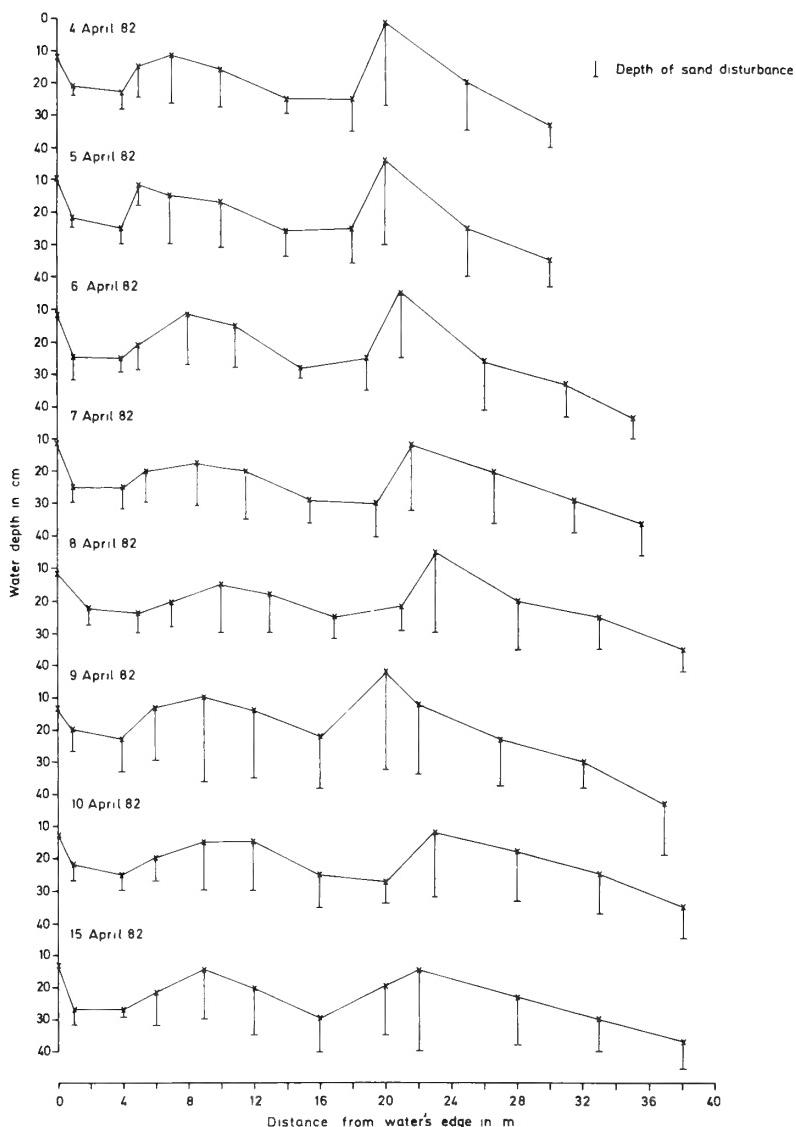
FIG. 3.   Nearshore morphology profiles in April 1982.

taken for logistical reasons. The intensive sampling period mainly referred to in this paper was seven consecutive days and one set of samples four days later, in early April, 1982.
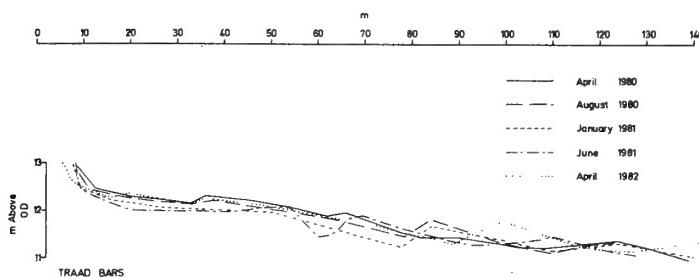
FIG. 4.   Variation in nearshore morphology over 2 years.

RESULTS

The nearshore morphology profiles for the period of intensive sampling are shown in Figure 3. There were two bars present at that time in the area sampled. Bar I, 7-8 m from the water's edge, varied between 0.1 to 0.18 m below water level, with a depth of sand disturbance on its crest of about 0.15 m (range 0.13 to 0.26 m). Bar II, 20-23 m from the water's edge was from 0.02-0.12 m below the water surface, with sand disturbance 0.25-0.3 m. There was very little apparent sand movement during the period of study, a time of exceptional calm when the wave height at breaking on Bar II barely exceeded 0.1 m. Figure 2 is a stylized diagram showing the stresses to which bars are subject in terms of wave energy and bottom shear stress. It is particularly evident that the latter is much higher on the crest of the bars. Figure 4 indicates the degree to which the sand bars can move, being nearshore profiles measured over a period of two years. Bar I was more often absent than present, Bar II, when present, varied horizontally over a distance of *c.* 3 m and vertically about 0.15 m. There are futher bars, not sampled during this study, for which the range of movement was greater.

The total chironomid fauna of the various inshore zones is shown in Table 1, where results from several sites have been grouped together. The nearshore area was the richest in species terms, with some e.g. *Endochironomus, Microtendipes,* which did not occur elsewhere on the transect. The inner bar (I) had quite a variety of species but no *Cladotanytarsus* or *Tanytarsus,* both of which reappeared between the bars. The outer bar (II) had the poorest fauna, followed by its lakeward side. The densities of the five most common species are shown (Fig. 5) but it must be remembered that confidence limits of there estimates are large, because of the small number of samples. *Paracladopelma* and *Stictochironomus* were generally the most abundant species, and the most widely distributed, although *Paracladopelma* was generally absent from Bar II and its im-
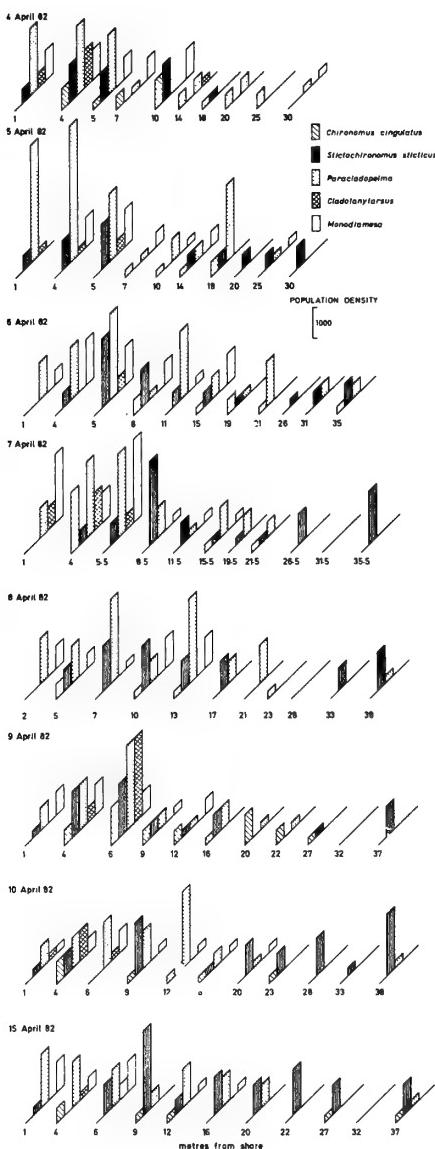
FIG. 5.   The density of the five most common species in April 1982.

Water depth and depth of sand disturbance at sampling points along transect

Distribution of fauna along transect.
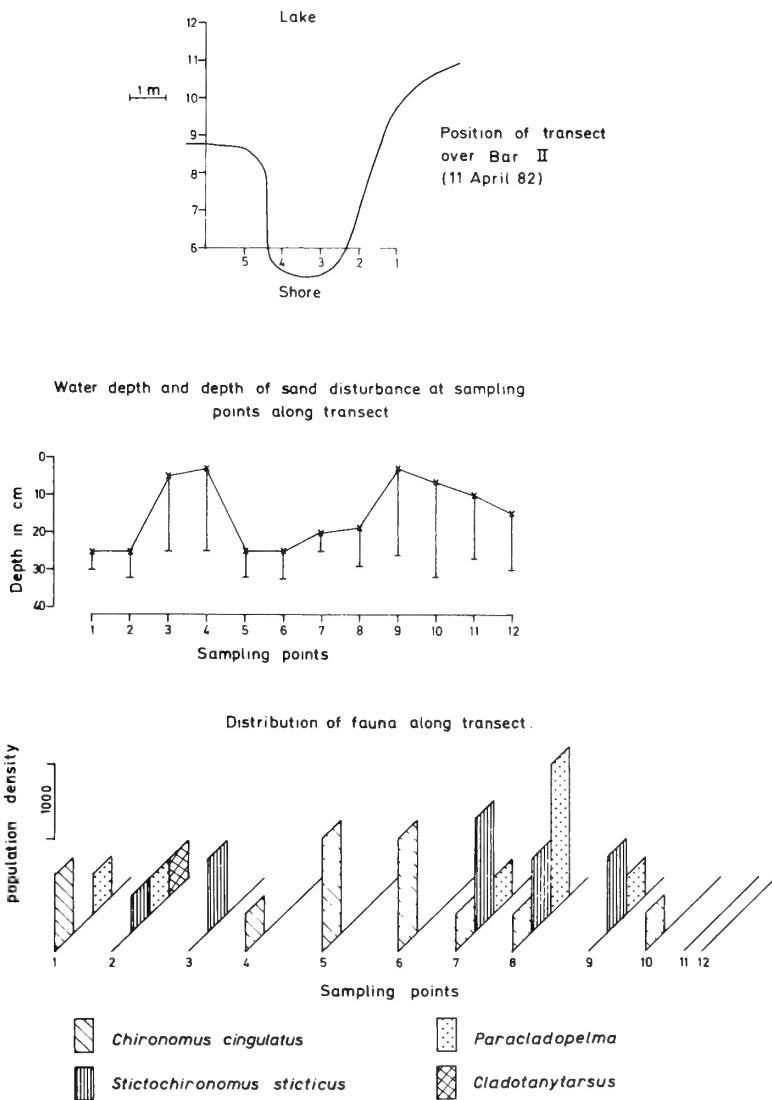
Fig. 6. Morphology and fauna of Bar II.

mediate lakeward slope. *Cladotanytarsus* was generally confined to sites 1-3, the most sheltered. *Chironomus cingulatus* was for no obvious reason, never found at site 1, but in at least small numbers at all other sites. *Monodiamesa* was present at sites 1-6, but very infrequent at other sites.

TABLE 1.   Chironomid fauna of the various inshore zones.

Inshore of Inner Bar (Sites 1-3)	Crest of Inner Bar (Site 4)	Between Bars (Sites 5-7)	Crest of Outer Bar (Site 8)	Lakeward of Outer Bar (Sites 9-11)
Chironomus cingulatus	C. cingulatus	C. cingulatus	C. cingulatus	C. cingulatus
Glyptotendipes	Glyptotendipes	Stictochironomus	Stictochironomus	Stictochironomus
Endochironomus	Stictochironomus	Paracladopelma	Paracladopelma	Procladopelma
Stictochironomus	Paracladopelma	Polypedilum		Monodiamesa
Microtendipes	Polypedilum	Cladotanytarsus		Orthocladius
Paracladopelma	Monodiamesa	Tanytarsus		Natarsia
Polypedilum	Potthastia	Monodiamesa		
Cladotanytarsus		Potthastia		
Tanytarsus		Natarsia		
Monodiamesa				
Orthocladius				
Potthastia				
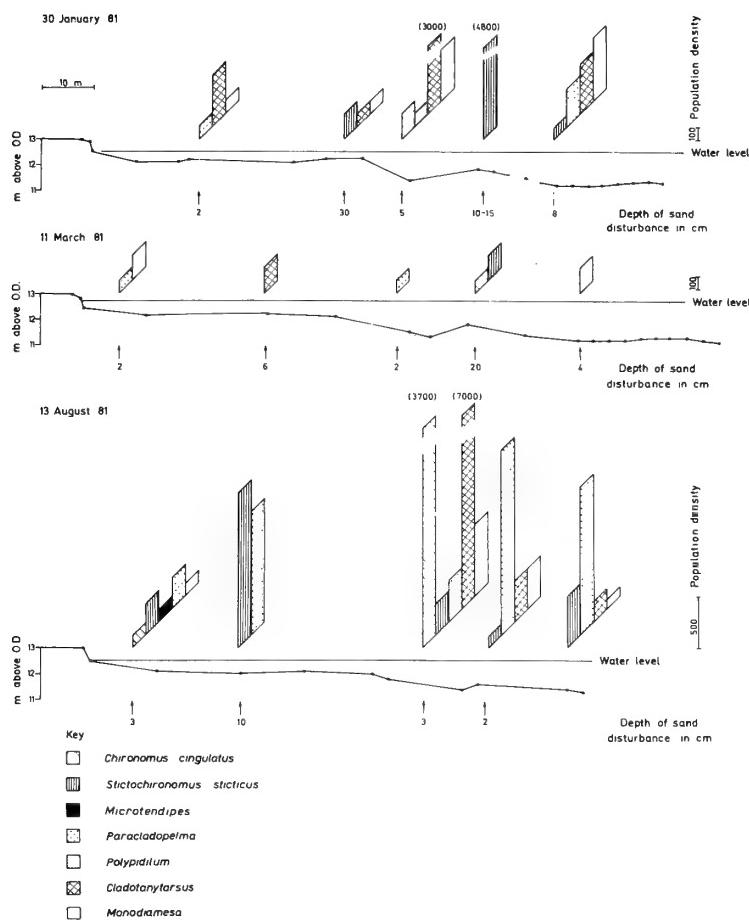
FIG. 7.   Fauna of the study area on selected dates in 1981.

Total abundance was generally greatest at sites 1-3, then, in order of decreasing abundance, 5-7, 4(Bar I), 9-11, 8(Bar II).

To investigate further the effects of a sand bar on the fauna, a transect was taken across Bar II, consisting of single cores taken at 1 m intervals (Figure 6). This shows very clearly the difference in sand disturbance between crest and trough, 20-25 cm on the crest and 5-7 cm in the trough. Most of the fauna was confined to the trough, only *C. cingulatus* and *Stictochironomus* appearing more than once on the crest.

To set the fauna in a longer term context, Figure 7 shows three profiles with associated fauna from 1981. In January, number of species was restricted but abundance of some was quite high. By March, the fauna was very depleted (emergence was unlikely to have been a factor in this) but the picture was quite different in August when most species had entered a new generation. Judging by the depth of the disturbed layer, sand disturbance had been minimal for a period so, presumably, allowing young larvae to settle. A further indication of the potential variety of the fauna in a sand habitat is shown by the deeper water sites off the beach and on the more sheltered north side of Traad Point (Table 2). Several species, e.g. *Cladotanytarsus,* reappear at 1 m depth and can be very abundant, indicating that they are not depth limited on the inner depth profile. *Microtendipes* is present in the deeper samples and is most abundant on the sheltered side of the point, while *Stictochironomus* is the opposite, more abundant on the beach side.

Discussion

The chironomid fauna of this sandy area of Lough Neagh is similar to that found in other lakes, e.g. Loch Leven (Maitland & Hudspith 1974). However, in an exposed place like Traad Beach, the fauna of the area from the inner bar (I) to the lakeward slope of Bar II is restricted both in species and numbers, and it is in this area that wave energy has its greatest effect on the lake bed, as can be seen in the profile of bottom shear stress. Different species react differently to this. *Cladotanytarsus* is restricted to the low energy zone inshore (sites 1-3), reappearing at depths of > 1 m where wave energy no longer causes sand disturbance. *C. cingulatus* distribution is not obviously related to sand disturbance; it is present at most sites along the profile, although it appeared to be less common at sites on the immediate lakeward slope of Bar II (9 & 10). Possibly, sustained disturbance is an adverse factor at these sites. *Stictochironomus* also shows no statistical relationship to depth of sand disturbance and is able to tolerate conditions at all sites on the transect, often attaining peak numbers on the crest of one of the bars. As it appears to be less successful when other species are present, lack of competition on the crest of the bars could be a factor. *Paracladopelma* and *Monodiamesa* can to some extent be considered together as their abundance is strongly correlated (correlation coefficient 0.51, significant at 1% level). Both give significant inverse relationships when regressed against depth of sand disturbance (D).

Paracladopelma $= 6.6842 - 0.2666D$
Monodiamesa $= 2.8854 - 0.1186D$

TABLE 2. Chironomid fauna and density in 1-2 m zone of Traad Beach and north Traad Point.

October 1981		No m^{-2}	
		Beach	Point
1 m.	C. cingulatus	1324	3366
	Stictochironomus	407	204
	Microtendipes	407	3060
	Glyptotendipes	102	1428
	Endochironomus	305	2958
	Limnochironomus		102
	Paracladopelma	305	
	Cryptochironomus 'defectus'	102	305
	Cladotanytarsus	7140	14586
	Tanytarsus	204	
	Monodiamesa	305	
	Natarsia	204	102
	Orthocladius		407
2 m.	C. cingulatus	509	407
	Glyptotendipes	1018	815
	Microtendipes	102	
	Endochironomus	1018	204
	Cryptochironomus 'defectus'		204
	Cladotanytarsus	10200	611
	Monodiamesa	611	102
	Orthocladius	102	
	Potthastia longimana	102	
March 1982			
1 m.	C. cingulatus	815	713
	Glyptotendipes		102
	Stictochironomus	407	
	Microtendipes		815
	Endochironomus		102
	Paracladopelma	102	1730
	Cryptochironomus 'defectus'	102	204
	Cladotanytarsus	305	10608
	Monodiamesa	204	305
	Orthocladius		204
2 m.	C. cingulatus		204
	Stictochironomus	204	102
	Endochironomus	407	305
	Cryptochironomus 'defectus'		102
	Cladotanytarsus		611
	Monodiamesa	509	
	Orthocladius		204

Both these lines intersect the X axis at about 25 cm, the average value found on the crest of Bar II, both species seeming able to tolerate the degree of disturbance on Bar I. Another species of note is *Microtendipes,* generally a common inshore species and occasionally found off Traad Beach (Figure 7) but usually confined to the deeper sites (Table 2) and perhaps unable to tolerate sand disturbance.

Similar factors to these have obviously been considered in relation to lotic fauna (Petran & Kothe 1978, Wiley 1978), but less often for lakes (but see Maitland 1979). Wiley (1981) did some experimental work on factors influencing the penetration of chironomid larvae into particular substrates and found that the burrowing behaviour of *Stictochironomus* and *Paracladopelma* was different. The former employed a "shovelling" motion and the latter a "jackhammer" approach, which reduced penetration time by 20%. He also found that body size affected penetration time. Work on similar lines might help to explain some of the distribution differences in lake chironomids. It is also possible that depth of occurrence in the sediment could also be important in tolerating sand disturbance. Wiley (1981) found this to be so for *Stictochironomus;* it avoided stream bed erosion by burrowing deeper into the sediment. Preliminary results with divided cores from Lough Neagh are inconclusive, but this is another possible line of enquiry.

In conclusion, it is obvious that the energy input on this small beach area is an important factor determining the distribution of the fauna, and that different species can tolerate different degrees of disturbance. Secondly, a point not much emphasized so far in this paper but nonetheless important, in exposed areas like this one, where there is a lot of sand movement, it is essential to understand the changing morphology of the lake bed when sampling, particularly whether samples are from bar or trough; otherwise interpretation of consecutive results from one site may be very difficult.

REFERENCES

CARTER R.W.G.   1983.   The geology, hydrology and sedimentology of Lough Neagh and its surrounding catchment. In Wood, R.B. and Smith, R. (eds.) Lough Neagh Monogr. Biol. (in press).

CARTER R.W.G. AND J.H. BALSILLIE. 1983. On the amount of wave energy transmitted over nearshore sand bars. Earth Surf. Proc. Landforms 8:

MAITLAND, P.S. 1979. The distribution of zoobenthos and sediments in Loch Leven, Kinross, Scotland. Arch. Hydrobiol. 85:98:125.

MAITLAND, P.S. AND P.M.G. HUDSPITH. 1974. The zoobenthos of Loch Leven, Kinross, and estimates of its production in the sandy littoral area during 1970 & 1971. Proc. Roy. Soc. Edin. 74B:219:239.

PETRAN, M. AND P. KOTHE. 1978. Influence of bedload transport on the macrobenthos of running waters. Verh. Internat. Verein. Limnol. 20:1867:1872.

WILEY, M.J. 1978. The biology of some Michigan trout stream chironomids (Diptera: Chironomidae). Mich. Acad. 11:193:209.

_____. 1981. An analysis of some factors influencing the successful penetration of sediment by chironomid larvae. Oikos 36:296:302.

Thoracic Chaetotaxy of Chironomid Pupae

(Diptera: Chironomidae)

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ABSTRACT. — Thoracic chaetotaxy was studied in pupae of 285 Chironomidae species belonging to 158 genera and nine subfamilies. The purpose of the study was to observe patterns of chaetotaxy present in the higher taxa and to determine if such patterns are indicative of trends throughout the family. The analysis included the setal groups present, the number of setae per group and the longitudinal placement of the Dcs and Sas. Intraspecific variation was found to be very low, both within and between populations. Sexual dimorphism was not apparent. Intrageneric variations were found but, basically, the species of a genus have the same groups and number of setae and the same relative placement. Although variations were considerable within some subfamilies, each subfamily appears to have a basic plan. Observed trends through the family include: (1) the movement of the supraalar seta to the position of the fourth dorsocentral; (2) the loss of metanotal setae; and (3) the development of anterior and posterior pairs of dorsocentral setae.

INTRODUCTION

As a continuation of my study of character states in chironomid pupae (Coffman, 1979), I am presenting in this paper the results of a comparative analysis of the number and distribution of thoracic setae. Although many authors have included thoracic setae in descriptions of pupae, the character states of most lower taxa are unknown and general patterns associated with most higher taxa have not been described in detail.

The purpose of this study is to determine, through the examination of a large number of species and genera, if patterns exist which are typical of higher taxa and if those patterns may be related by trends throughout the family.

METHODS AND MATERIALS

Slide mounted pupal exuviae representing 285 species, 158 genera and eight subfamilies were used in the analysis (Table 1). Character states for Aphroteniinae were determined from Brundin (1966). When possible,

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TABLE 1.   Number of Chironomidae genera and species examined for chaetotax of the thorax.

TAXA	NO. OF GENERA	NO. OF SPECIES
TELMATOGETONINAE	1	1
TANYPODINAE	24	31
COELOTANYPODINI	(1)	(1)
MACROPELOPIINI	(7)	(11)
NATARSINI	(1)	(1)
PENTANEURINI	(14)	(16)
TANYPODINI	(1)	(2)
PODONOMINAE	7	8
BOREOCHLINI	(4)	(4)
PODONOMINI	(3)	(4)
BUCHONOMYIINAE	1	1
DIAMESINAE	13	20
BOREOHEPTAGYIINI	(1)	(1)
DIAMESINI	(8)	(15)
HEPTAGYINI	(3)	(3)
PROTANYPODINI	(1)	(1)
PRODIAMESINAE	(3)	(4)
ORTHOCLADIINAE	54	118
CHIRONOMINAE	55	102
CHIRONOMINI	(42)	(70)
PSEUDOCHIRONOMINI	(1)	(6)
TANYTARSINI	(12)	(26)
TOTAL	158	285

several specimens of each species were examined to verify the chaetotaxy. The terminology for the groups of setae analyzed is slightly modified from Saether (1980): MAps-median antepronotal seta(e); LAps-lateral antepronotal seta(e); Pcs-precorneal seta(e); Pas-prealar seta(e); Dcs-dorsocentral seta(e); Sas-supraalar seta(e); Mns-metanotal seta(e) (Fig. 1). The number of setae in each group was determined and the position of the Dcs and Sas on the longitudinal axis measured with an occular micrometer. The longitudinal position of these setae was determined as the distance to each of the setae from the anteromedial angle of the antepronotum along a line extending to the most posterior part of the thorax (Fig. 1). Dorsoventral position was not measured and differences in size (diameter and length), branching and pigmentation were not systematically studied.

RESULTS AND DISCUSSION

Intraspecific variation—The validity of this analysis would be severely restricted if the number and/or location of setae varied greatly at the species

TABLE 2.   Intrapopulation variation in the longitudinal position of the Dcs of *Tvetenia* cf. *calvescens*. All specimens from Linesville Creek, Pa. (position of setae expressed as percent of thorax length from the anteromedian angle).

SEX	DATE	Dcs1	Dcs2	Dcs3	Dcs4
female	9 July 70	32.5	35.2	56.9	57.4
female	21 July 70	33.7	35.3	57.7	59.1
male	17 Aug. 70	33.3	36.1	58.8	59.4
male	17 Sept. 70	33.4	36.1	56.1	56.5
male	17 Oct. 70	33.2	34.3	57.5	59.7
female	30 Nov. 70	33.7	34.9	57.7	58.9
female	14 Apr. 71	34.8	35.8	54.2	54.8
female	15 May 71	31.3	33.5	53.7	54.7
female	15 June 71	37.6	39.1	58.6	59.0
male	6 July 71	35.5	38.5	60.7	61.5
	X =	33.9	35.9	57.2	58.1
	S.D. ±	1.7	1.7	2.1	2.2

TABLE 3.   Interpopulation variation in the longitudinal position of the Dcs of *Tvetenia* cf. *calvescens*. (Position expressed as in Table 2).

LOCALITY	Dcs1	Dcs2	Dcs3	Dcs4
Alaska	34.5	36.9	58.3	58.6
Maine	33.0	34.3	56.3	56.3
Michigan	32.1	34.2	56.6	57.6
New York	35.4	38.2	58.0	58.0
Oregon 1	34.6	37.2	56.4	57.7
Oregon 2	33.2	35.5	56.1	58.4
Pennsylvania 1	31.6	32.9	54.4	55.2
Pennsylvania 2	33.5	34.7	55.9	56.9
Wyoming 1	32.1	34.6	56.4	57.2
Wyoming 2	31.7	34.0	53.9	56.3
X =	33.2	35.3	56.2	57.2
S.D. ±	1.3	1.7	1.4	1.1

level as a function of sex, size or season. To test for such variation, ten exuviae of the common and widespread *Tvetenia* cf. *calvescens,* including males and females of different sizes collected in eight different months from Linesville Creek, Pennsylvania were analyzed for number of setae in each group and position of the Dcs. There was no variablility in the groups of setae or number of setae per group. The data for the position of the Dcs demonstrate that regardless of sex, size or season these setae are constant in

TABLE 4. Intrageneric variation in the longitudinal position of the Dcs. (Data are mean values for position, S.D. in parentheses after each value; position expressed as in Table 2).

TAXON	# OF SPP.	Dcs1	Dcs2	Dcs3	Dcs4
Cricotopus s.1	9	40.6(2.1)	44.4(4.0)	55.8(3.0)	58.0(3.6)
Eukiefferiella	11	37.7(3.8)	42.6(5.7)	57.0(3.4)	61.7(3.5)
Orthocladius s.1	22	40.7(2.0)	47.4(4.3)	53.3(3.2)	56.1(3.2)
Pseudochironomus	6	33.7(3.2)	34.4(3.3)	57.0(3.1)	57.8(3.0)
Cryptochironomus	5	38.6(6.1)	40.8(6.9)	52.3(6.3)	55.3(5.3)

position (Table 2). An additional ten specimens of *T.* cf. *calvescens,* collected from ten locations spanning 20 degrees of latitude, 80 degrees of longitude and 3000 meters in elevation, were analyzed to determine if there is a significant geographical component to thoracic chaetotaxy at the species level (Table 3). The groups of setae present and the number of setae per group did not vary in any of these specimens and the mean positions of the Dcs were essentially identical to the Linesville Creek values. It may be inferred from these results, which are similar to those from other species examined, that the chaetotaxy of the thorax is extremely constant at the species level.

Intrageneric variation—As might be expected, the number and location of setae does vary among the species of a genus. This may be illustrated using the genera *Cricotopus, Eukiefferiella, Orthocladius, Pseudochironomus* and *Cryptochironomus* (Table 4). Most of the variations in position of the Dcs result from longitudinal shifts of all four or, at least,most of the four, thereby retaining their relative positions. Some species may have additions to or deletions from the "typical" number in the other groups of setae. Basically, however, the species of a genus have the same groups of setae, the same number per group and the same relative position of the Dcs. Variations in chaetotaxy may, in many instances, prove to be of taxonomic importance for species and generic level taxa.

Variations in higher taxa—Considering the over-all ecological and structural heterogeneity characteristic of most tribes and subfamilies (at least the larger ones), it is somewhat surprising to find that most members of a particular taxon demonstrate a remarkable degree of similarity in groups of setae present, number of setae in each group (Table 5) and the longitudinal positions of the Dcs and, when present, Sas (Table 6). The over-all pattern of chaetotaxy for these higher taxa and the variations encountered within often appear to have taxonomic and phylogenetic significance.

Trends throughout Chironomidae—Discussion of trends at the family level is based on the data contained in Tables 5 and 6.

TABLE 5. Chaetotaxy of chironomid pupae by subfamilies and tribes. (Values are number of setae per group).

TAXON	MAps	LAps	Pcs	Pas	Dcs	Sas	Mns
TELMATOGETONINAE	1	0	2	0	3	1	2
TANYPODINAE	1	2(1)[a]	0-1[b]	0	2	1	1
Anatopyniini[c]	1	2[d]	0	0	2	1	1
Coelotanypodini	1	2	0	0	2	1	1
Macropelopiini	1	2(1)	0	0	2	1	1
Natarsini	1	2	1	0	2	1	1
Pentaneurini	1	2	1	0	2	1	1
Tanypodini	1	0[d]	0	0	2	1	1
PODONOMINAE	1-2	2(3)	3(2)	0(1)	3	0-1	4(3)
Boreochlini	1-2	2(3)	3	0(1)	3	0-1	4(3)
Podonomini	2	2	3(2)	0	3	0-1	4(3)
APHROTENIINAE[c]	1	2	1(2)	0	3	1	2
BUCHONOMYIINAE	3	2	3	0	1	1	2
DIAMESINAE	1-2	1(0,2)	3(2)	0(1,2)	3(0,1,2)	1(0)	1(0,2,5)
Boreoheptagyiini	1	2	3	2	3	1	1
Diamesini	2-1	1	3(2)	0(1)	1-2-3	1	1-2
Heptagyini	1	1-0	2	0	0	0	0
Protanypodini	6	1[e]	3	0	3.	1	5
PRODIAMESINAE	2	2	3	1	4	0	0
ORTHOCLADIINAE	2(3)	1-2(3)	3(2,1)	0(1,2)	4(3)	0	0(1)[f]
CHIRONOMINAE	1-2	0-1(2)	2-3	0	4(2)	0	0
Chironomini	1	0-1	2(3)	0	4(2)	0	0
Pseudochironomini	2	0	3	0	4	0	0
Tanytarsini	1	1(2)	3(2)	0	4	0	0

a = Values in parentheses indicate a rare character state.
b = Values following a dash indicate additional common character states. These are given in order of frequency of occurrence.
c = Data taken from the literature.
d = Values given may not be correct.
e = *Protanypus* possesses an additional group of setae near the LAps.
f = I have seen an Mns only in species of *Chaetocladius*.

MAps—There is no obvious trend in the number of MAps. Considered as a whole one MAps seems to be the basic number, although there are many exceptions to this. Tanypodinae never have more than one and it is always slightly posterior of the antepronotum, a condition which appears to be apomorphic for that subfamily. Three MAps are encountered in a few Orthocladiinae and in Buchonomyiinae. *Protanypus* is unique with six. The number in all Chironomini and Tanytarsini examined was one, apparently representing a reduction from the presumed ancestral condition of at least two MAps found in all Prodiamesinae and Orthocladiinae. It is interesting

TABLE 6. Number and longitudinal spacing of Dcs in chironomid subfamilies. (Generic means are given for positions and are expressed as in Table 4).

TAXON	# OF GENERA	Dcs1	Dcs2	Dcs3	Dcs4-Sas
TELMATOGETONINAE	1	39.2	44.2	48.6	45.0[a]
TANYPODINAE	24	46.6(3.5)	50.2(5.2)	none	66.3(5.3)[b]
PODONOMINAE	7	43.4(6.2)	48.0(6.3)	55.3(6.0)	67.8(2.6)[b]
APHROTENIINAE	—	not measured			
BUCHONOMYIINAE	1	40.9[d]	45.3[d]	56.3	65.6[b]
DIAMESINAE	10	38.5(3.2)	45.1(5.0)	51.8(4.0)	69.1(4.0)[b]
PRODIAMESINAE	3	39.2(4.3)	44.0(1.7)	53.1(5.4)	59.5(5.6)[c]
ORTHOCLADIINAE	54	39.7(4.8)	44.8(6.2)	53.2(5.7)	56.6(4.8)[c]
CHIRONOMINAE	55	37.6(4.1)	40.9(5.5)	54.2(5.2)	55.9(4.3)[c]

a = Sas is anterior of "typical" position.
b = Sas in "typical" position.
c = No Sas, presumably the homologous seta is in the Dcs4 position.
d = Position of setal scar.

to note that Pseudochironomini is the only tribe of this subfamily to have two MAps. Given the present understanding of phylogenetic relationships within Chironominae, this would imply either the parallel reduction to one MAps in Chironomini and Tanytarsini or a reduction to one in the ancestor of the Chironominae and a secondary increase to two MAps in Pseudochironomini.

LAps—The number of setae in this group varies widely throughout the family and there is no obvious trend. *Protanypus* is unique in having an additional group of setae posterior to the LAps.

Pcs—The basic number of setae in this group is two or three but a number of exceptions occur, especially in Tanypodinae which never have more than one. There is no obvious trend.

Pas—The most common condition is for Pas to be absent. This is presumably the case for all of the Telmatogetoninae, Tanypodinae, Aphroteniinae, Buchonomyiinae and Chironominae. The only Podonominae that I have seen with a Pas is *Trichotanypus*. One Pas occurs in all Prodiamesinae and one or two Pas are found sporadically in Diamesinae and Orthocladiinae. Apparently no Chironominae have Pas.

Dcs-Sas (Figs. 2-12)—If the most ventral seta of Telmatogetoninae is a Sas, although it is anterior of the "typical" position, then all Telmatogetoninae (Fig. 2), Tanypodinae (Fig. 3), many Podonominae (Fig. 4), all Aphroteniinae (Brundin, 1966; Figs. 493, 494, 515, 517), Buchonomyiinae (Fig. 5) and most Diamesinae (Fig. 6) possess a Sas. This seta is absent in all Prodiamesinae (Fig. 7), Orthocladiinae (Fig. 8) and Chironominae (Figs. 9-12). The fact that Sas never occurs in taxa with four Dcs is considered as evidence that Sas is homologous to Dcs4. The trend that would seem to be evident involves the movement of Sas of the plesiomorphic subfamilies into the position of Dcs4 in the more apomorphic subfamilies.

Another trend in the longitudinal distribution of the Dcs is the development of an arrangement of these setae into anterior and posterior pairs. This pattern is found in all Prodiamesinae (Fig. 7), many Orthocladiinae (Fig. 8) and all Chironominae (Figs. 9-12). Although the paired pattern is common in Orthocladiinae, other patterns are not rare, for example: (1) three anterior and one posterior; (2) one anterior and three posterior; (3) all four evenly and widely spaced; (4) all four grouped closely together. The two pair pattern is most developed in the Chironominae (Figs. 9-12). All of the Tanytarsini (Fig. 9) and Pseudochironomini (Fig. 10) that I have observed not only have the two pair arrangement but, the members of the pairs insert contiguously. This condition is also found in almost all of the genera of the Chironomini of Saether (1977, Fig. 62) from *Paratendipes* through
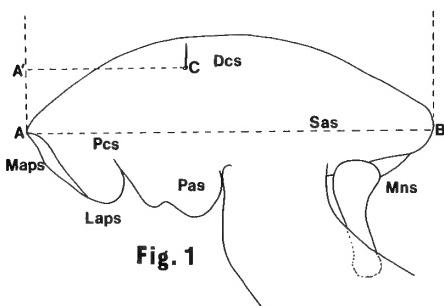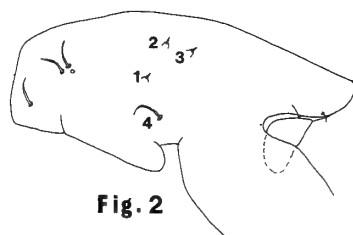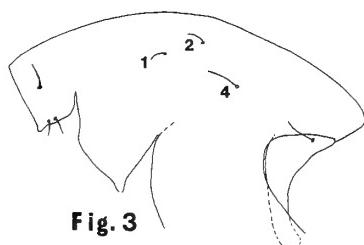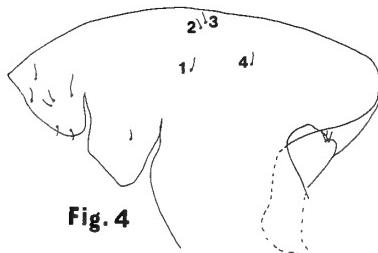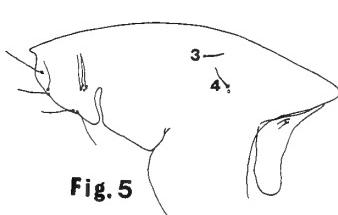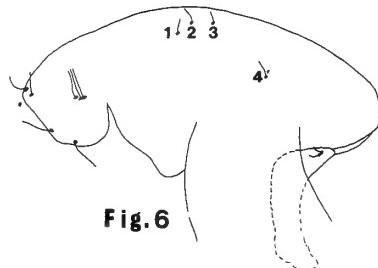
FIGS. 1-6:   FIG. 1.   Left half of generalized chironomid thorax with groups of setae located (see text for terminology of setae and measurement technique). A = anteromedian angle of thorax; B = posterior angle of thorax; A′ = point of origin for measurement of longitudinal position of seta C: FIGS. 2-6.   Left half of thorax illustrating chaetotaxy: 2. *Telmatogeton japonicus;* 3. *Macropelopia* sp.; 4. *Trichotanypus* sp.; 5. *Buchonomyia thienemanni;* 6. *Pagastia* sp. (Dcs1-4 indicated, Sas, when present, labeled as Dcs4).

Stenochironomus. It would seem, therefore, that the two pair pattern in which members of the pairs are contiguous is an apomorphic trait of Chironominae and that the secondary separation of the pair members in the genera of the *Chironomus* and *Harnischia* complexes is apomorphic for those groups.
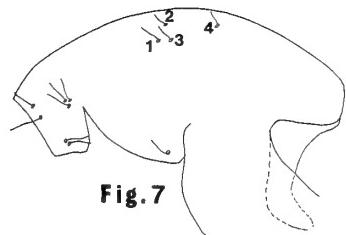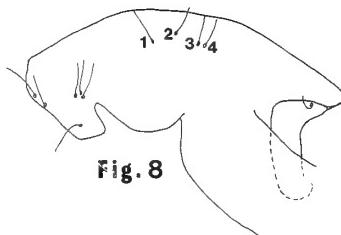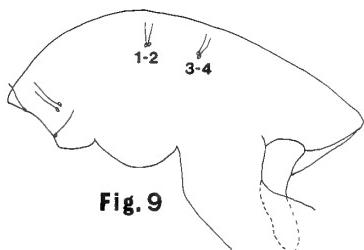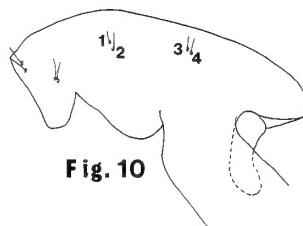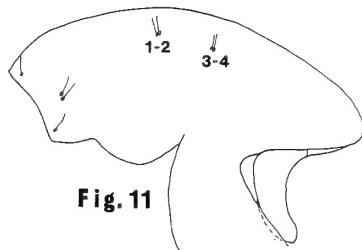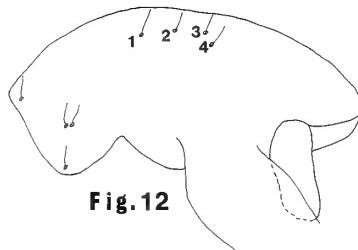
FIGS. 7-12.   Left half of thorax illustrating chaetotaxy: 7. *Prodiamesa* sp.; 8. *Chaetocladius* sp.; 9. *Rheotanytarsus anomalous* gr. sp.; 10. *Pseudochironomus* sp.; 11. *Polypedilum* sp.; 12. *Parachironomus* sp. (Dcs1-4 indicated).

Mns—At least one Mns is, apparently, present in all Telmatogetoninae, Tanypodinae, Podonominae, Aphroteniinae and Buchonomyiinae. It is also present in all Diamesinae except members of the tribe Heptagyini which lack most thoracic setae. In subfamilies Prodiamesinae, Orthocladiinae and Chironominae I have seen a Mns only in species of the orthoclad genus *Chaetocladius*. P. Cranston (pers. communication) has seen one in a species of O. (*Eudactylocladius*) but I have not been able to verify this with Nearctic material. This trend is strengthened by the observations that the location of the Mns in Telmatogetoninae through Buchonomyiinae is on that part of

the metanotum that forms the base of the haltere sheath. In Diamesinae the Mns are usually more medially located on the flat surface of the metanotum. Occasionally in Diamesinae and in *Chaetocladius* the Mns are much dislocated medially and have a different shape. The latter may not be homologous to the Mns of other taxa.

Conclusions

1. At the species level, thoracic chaetotaxy is remarkably constant in groups of setae present, number of setae in each group and longitudinal positions of the Dcs.

2. At the generic level, variations in chaetotaxy may be significant from one species to another but, in general, the pattern within a genus is constant and has taxonomic value.

3. Variations in chaetotaxy at the tribe and subfamily levels may be considerable but each of the higher taxa has a typical pattern. These patterns have taxonomic and possible phylogenetic significance.

4. At the family level the following trends are evident:

a. the movement of Sas of Telmatogetoninae, Tanypodinae, Aphroteniinae, Podonominae, Buchonomyiinae and Diamesinae to the Dcs4 position in the other subfamilies.

b. the development of anterior (Dcs1 and Dcs2) and posterior (Dcs3 and Dcs4) pairs of Dcs in Prodiamesinae, Orthocladiinae and Chironominae and, in particular, the very close proximity of the members of these pairs in Tanytarsini, Pseudochironomini and the plesiomorphic Chironomini.

References Cited

COFFMAN, W.P.   1979.   Neglected characters in pupal morphology as tools in taxonomy and phylogeny of Chironomidae (Diptera). *In:* O.A. Saether, (ed.): Recent developments in chironomid studies (Diptera: Chironomidae). Ent. scand. Suppl. 10:37-46.

BRUNDIN, L.   1966.   Transantarctic relationships and their significance as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. K. Svenska Vetensk Akad. Handl. 11:1-472.

SAETHER, O.A.   1977.   Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. Bull. Fish. Res. Bd. Can. 196:209 pp.

————.   1980.   Glossary of chironomid morphology terminology (Diptera: Chironomidae). Ent. scand. Suppl. 14:51 pp.

Chironomid Haemoglobins: Their Detection and Role in Allergy to Midges in the Sudan and Elsewhere.

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ABSTRACT. — Studies on allergic reactions of humans to chironomids, particularly to nuisance midges in the Sudan, are reviewed. Evidence is presented that chironomid haemoglobins are important allergens, a finding which indicates that chironomid midges should be seen as significant environmental allergens.

INTRODUCTION

Massive swarms of non-biting midges (Diptera: Chironomidae) emerge from the Sudanese Nile in the winter months (Lewis, 1956; Cranston *et al.,* 1981), and, according to Lewis (*loc. cit.*), appear to have done so since the 1920s. The swarms which are a most serious nuisance to man and livestock, restrict outdoor activity and may, in extreme cases, cause asphyxia. These swarms consist largely of *Cladotanytarsus lewisi* (Freeman, 1950), although other species of Chironomidae may also occur in large numbers (Lewis, 1956; Wülker, 1963; Cranston *et al.,* 1981). In order to understand the biology of these nuisance midges, Lewis (1956, 1957) and Lewis *et al.,*

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(1954) studied aspects of Nilotic chironomid life histories and fluctuations in numbers of adult midges attracted to lights. Attempts to control the midges using DDD and DDT as larvicides were reported by Brown *et al.* (1961), but fish mortality was high and the subsequent reduction in midge numbers cannot be interpreted as effective insecticidal control without detailed knowledge of normal population fluctuations. This need for "thorough baseline studies" was observed by Wülker (1963) when investigating biological control as a possible alternative mechanism for alleviation of the midge problem.

Apart from the nuisance caused by midge swarms, the association of human allergic reactions, such as asthma and allergic rhinitis with seasonal midge emergence has long been suspected (Kirk, 1952, 1953). In more recent years detailed investigations into the nature and extent of chironomid allergy in the Sudan have taken place. Particular emphasis has been given to the relationship between the epidemiological, entomological and immunological aspects of the problem. The nature and results of these multidisciplinary investigations are reviewed below. These studies, together with those of other researchers, indicated that chironomid haemoglobins are important allergens for humans. Therefore, the second part of the paper details our investigations into the role of these haemoglobins in the Sudanese midge allergy and discusses the belief that chironomid midges are more than a local Sudanese problem, being potentially a world-wide cause of allergy.

BACKGROUND

Strong evidence for the association between midges and seasonal human allergic reactions was provided by Kay *et al.* (in press a), who compared the prevalence of allergic symptoms in two Sudanese villages. An epidemiological survey was made of the population of Kalakla, a Nilotic village with midge problems, and contrasted with a similar survey of Umm Dawa Ban, a desert village some 40 kms east of Khartoum, distant from the Nile and without midge problems. The results indicate that allergic rhinitis occurred at a rate of 6.7% in Kalakla and 1.5% in Umm Dawa Ban. The percentage of those surveyed with asthma in addition to allergic rhinitis, was four times greater in Kalakla than in the control village. The sufferers' own assessment of the provoking agents indicate that winter seasonal exposure to chironomid midges was a major aetiological factor in asthma and rhinitis in Kalakla. Kay *et al.,* (in press) concluded that repeated exposure to chironomids results in a very high incidence of allergic rhinitis, as well as increasing significantly the indigenous asthmatic population.

The geographical distribution of midge induced allergy was considered by Lewis (1956) who recorded the problem in Khartoum and Wadi Halfa, and by Satti & Abdel Nur (1974) who suggested that problems of nuisance midges and allergy might occur as far north as Lake Nasser (Lake Nubia or Lake Aswan). In an attempt to obtain further information on the geographic extent of hypersensitivity to chironomid midges, Cranston *et al.* (in press) performed skin tests with unfractionated ('crude') *C. lewisi* extracts on asthmatic subjects living close to the Nile in Sudan and Egypt. Hypersensitive individuals were found on the White Nile as far south as Kosti, on the Blue Nile as far east as Sennar, and on the Nile as far north as Aswan, Luxor and Qena in Upper Egypt (Cranston *et al.*, in press). The problem appears not to occur in middle and Upper Egypt (Dr. Soliman Diaa el Din, *pers., comm.;* ms in prep.).

The evidence of the epidemiological survey of Kay *et al.* (in press) and the geographical distribution studies indicate that the exposed population numbers hundreds of thousands, and the number expected to suffer from midge related allergic problems must be in the tens of thousands.

C. lewisi is always the dominant species of chironomid in samples of midges collected in the areas of Sudan most affected by nuisance midges. Four species, *Dicrotendipes fusconotatus* (Kieffer), *Conchapelopia cygnus* (Kieffer), *Procladius noctivagus* (Kieffer) and *Nanocladius vitellinus* (Kieffer), were also present in all catches. Although these subdominant species underwent similar daily changes in abundance in light-trap catches as did *C. lewisi* the greater the total daily catch the greater was the proportion of *C. lewisi* until in the largest catches of over a quarter of a million individuals per trap per night, the proportion of *C. lewisi* was over 95% of the total catch (Cranston *et al.,* 1981).

Lewis (1956, 1957) made the only detailed study of the biology of *C. lewisi* and observed that the midge nuisance seemed to be associated with the construction of dams and the subsequent increase in lacustrine conditions in the Nile. Cranston *et al.* (1981) confirmed and strengthened this hypothetical relationship and suggested that the summer seasonal rains in the catchment areas of the White and Blue Niles caused a natural eutrophication of the river by washing in of plant nutrients, particularly nitrates, phosphates and silicates. After the period of maximum flow in the river, turbidity decreases in the extensive slow-flowing areas caused by natural and man-made damming of the Nile. As a result, the increased light and high plant nutrient levels allow abundant algal and diatom growth which provides a food source for many chironomid larvae. *C. lewisi* larvae, shown to be benthic grazers of diatoms and algae and presumed to have a rapid life cycle, make maximum use of this seasonally abundant food

resource. This results in a subsequent large increase in adult midge numbers. Cessation of midge emergence in the Spring seems to coincide quite closely with the crash in algal numbers following nutrient depletion. Further evidence supporting this theory is seen when altered hydrological conditions occur, such as reduced or sporadic rainfall or alterations in the flow regime of the Nile. These factors which occurred in the period 1980-82 were associated with a reduction of the duration and severity of the midge season.

It is significant that the factors which lead to the development of very high populations of midges in the Sudan are not unique to this ecosystem, but occur in many bodies of water throughout the world.

Further evidence for the association between chironomid midges and allergic reactions in Sudanese people has been provided by immunological investigations. Comparison of patients' symptomatology (severity of bronchial asthma and/or allergic rhinitis) with daily numbers of midges assessed by light-trap catches, indicated a relationship. During periods of minimal midge emergence allergic symptoms tended to be reduced, but increased during moderate to large emergences of up to 400,000 midges per trap per night. A massive emergence comprising over 99% *C. lewisi* during December 1979, not sampled quantitatively but estimated to contain the equivalent of well in excess of half a million midges, was clearly associated with severe signs and symptoms of immediate-type hypersensitivity, including bronchospasm and rhinitis (Kay *et al.*, 1983).

Kirk (1952) showed that a number of Sudanese bronchial asthmatics gave a high proportion of strongly positive responses when skin tested with crude extracts of midges. This skin test reactivity was confimed by Kay *et al.* (1978) who also showed that sera from *C. lewisi*-sensitive Sudanese caused passive sensitisation of lung fragments which led to IgE (immunoglobulin E) — mediated release of histamine and SRS-A (slow reacting substance of anaphylaxis). The development of a radioallergosorbent test (RAST) by Gad El Rab & Kay (1980) allowed quantitative measurement of specific IgE present in serum, and was used to demonstrate a relationship between RAST scores and the severity of patients' symptoms.

In order to test if *C. lewisi* alone was responsible for midge hypersensitivity in the Sudanese, patients previously shown to be hypersensitive to extracts of pure *C. lewisi* were skin 'prick' tested with extracts of seven of the subdominant species of Nilotic Chironomidae. The results indicated that *C. lewisi* was the most important species, but that there was limited crossreactivity with some other species, particularly *Dicrotendipes fusconotatus, Procladius noctivagus* and *Conchapelopia cygnus* (Cranston *et al.*, in press).

Confirmation of the aetiological role of chironomid midges, particularly *C. lewisi,* in allergic problems in the Sudan, led to attempts to characterise the major allergens involved (Gad El Rab, Thatcher & Kay, 1980; Tee *et al.,* in press). Fractions from Sephadex G100 gel filtration and ion exchange chromatography were assayed for antigenicity by skin testing hypersensitive individuals. These techniques indicated that a major proportion of the allergenic material was associated with a molecular weight of 15-20,000 daltons and a pI of 4.3. More definitive techniques, still using Sephadex G100 gel filtration but including RAST inhibition and autoradiography with ^{125}I-anti-IgE, showed that the 'major peak' of allergenicity was associated with molecules of approximately 17,000 daltons and with a pI range of 3.5 to 5.5. The major allergens from *C. lewisi* therefore appear to be a group of closely related acidic peptides.

Contemporaneously with the revival of interest in midge allergy in the Sudan, Baur and his colleagues in West Germany were investigating the incidence of hypersensitivity and respiratory allergy amongst workers occupationally exposed to freeze-dried larvae of *Chironomus riparius* (cited as *Chironomus thummi thummi* (CTT), but see synonymy by Credland, 1973). Using RAST and RAST inhibition, Baur *et al.* (1982) showed that the antigenic determinants were sited within peptide sequences in some of the 11 polymorphic forms of haemoglobin present in CTT, and that specific antibody against haemoglobins accounted for a proportion of the total IgE of hypersensitive individuals. The first indications that there might be antigens common to both the German occupational allergy and to the Sudanese environmental allergy came from Baur (1982) and Baur *et al.* (1982). They found that the sera of Sudanese hypersensitive to *C. lewisi* gave positive RAST results in tests with CTT larvae and adults, with isolated total CTT haemoglobin and with one of the antigenic peptide sequences.

The implications of an allergen or group of allergens common to two genera of chironomids which are phylogenetically distantly related, are considerable, in view of the ubiquity and abundance of the Chironomidae. Thus it was important to establish whether haemoglobin was one of the major allergens in the Sudanese midge allergy. It became necessary to extend the range of diagnostic skin tests on *C. lewisi* sensitive individuals to try to test these ideas. Extracts were prepared from larvae and pupae of *C. lewisi* and from larvae and adults of *Ch. riparius* (=CTT) and used in skin testing together with a haemoglobin extract from CTT provided by Dr. X. Baur, and with four allergenic fractions derived from Sephacryl S200 by gel filtration and rechromatography from *C. lewisi* extract. The methods of preparation of the extracts, results of skin tests and interpretation of the results are presented below.

Since the results are dependent on quantification of skin 'prick' test responses, it was necessary to establish the relationship between these responses and the actual levels of specific anti-*C. lewisi* IgE present in patients' sera. RASTs were performed on the serum from each patient following a skin test with unfractionated *C. lewisi* extract and the relationship examined.

<div align="center">MATERIALS AND METHODS</div>

Radioallergosorbent test (RAST). — A relationship between the percentage binding of ^{125}I-anti-IgE to allergen polymer complex (the RAST value) and the severity of clinical symptoms of *C. lewisi* hypersensitive individuals was demonstrated by Gad El Rab & Kay (1980). In order to demonstrate whether there was a similar relationship between the severity of skin test response and the specific IgE directed against *C. lewisi* antigen(s), RAST tests were performed on the sera of 40 Sudanese individuals previously shown to be skin test sensitive to unfractionated *C. lewisi*. A group of 24 skin test negative individuals from the United Kingdom, who had not been exposed to *C. lewisi,* were selected as controls, and their sera were similarly subject to RAST testing. The basis for this method of allergen determination is given by Wide *et al.* (1967).

(i) *Preparation of Allergen Polymer Complex (APC).* — Ten mg of lyophilised, unfractionated *C. lewisi* extract was coupled with each gram of CNBr-activated Sepharose 4B (Pharmacia).

(ii) *RAST assay.* — Optimum conditions for the RAST assay were determined as two 16 hour incubations with 50µl of serum and 100 µl of APC (6.25% concentration) in the first incubation, and 50 µl ^{125}I-anti-IgE (Pharmacia) in the second. Cord blood sera with no demonstrable IgE were used in all assays as negative controls.

Skin 'prick' testing. — Patients shown previously to be hypersensitive to unfractionated *C. lewisi* extracts by skin test or RAST test, or both, and who had been recruited for clinical trials in Khartoum, Soba or Kalakla clinics, were selected for two further series of tests. In one group 16 patients were tested with unfractionated extracts of *C. lewisi* adults, pupae and larvae. In another group, 26 different patients were tested with unfractionated *C. lewisi* adult extract, four S200 fractions of adult *C. lewisi,* three unfractionated extracts of *Chironomus riparius* and with *Ch. riparius* haemoglobin. Skin 'prick' tests were performed on the volar region of the forearm, and maximum and minimum diameters of any resultant weals were measured 15 minutes after the test. All patients selected gave a

response of at least 4mm by 4mm to the histamine control and of at least 2mm by 2mm to the unfractionated *C. lewisi*. Patients who gave any significant response to the negative control were not selected for further tests.

All skin 'prick' test responses were calculated as a weal 'area' by multiplying the maximum and minimum diameters of each weal and subtracting any weal 'area' provoked by the negative control. In 23 cases from the group of 26, skin 'prick' tests were duplicated in the reverse sequence on the opposite arm; in these cases the average response to each antigen was calculated. Antigenic material for the skin tests was obtained as follows:

(i) *Collection of midges*. — Adult midges were collected by light-trap at Kalakla in the Sudan and identified as comprising over 99% *C. lewisi*. These were dried at 26°C and stored at 4°C in sealed plastic bags. Larvae and pupae of Nilotic Chironomidae were collected by aquatic drift nets partially immersed in the White Nile at Khartoum. The samples, comprising up to 75% *C. lewisi*, were dried on filter paper at 26°C and stored at 4°C.

Larvae and adults of *Chironomus riparius* were collected from cultures maintained by Dr. P. Credland and dried as before. A commercially available tropical fish food containing predominantly *Ch. riparius* larvae, killed by ultraviolet radiation, packed by "Gamma Foods", was purchased from an aquarists' shop and dried as above. The provenance of these larvae is unknown.

(ii) *Preparation of extracts*. — A known weight of each sample of adult, pupal or larval midge was defatted in three changes of ether over 24 hours. Extractions were performed in Coca's solution (5g sodium chloride, 2.75g sodium bicarbonate and 4g phenol, made up to 1 litre with distilled water) for 48 hours at room temperature. The midges were removed by filtration and the filtrate centrifuged at 18,000g for 40 minutes. The supernatant was passed through a 0.45μ Millipore filter (Millipore Ltd., Bedford, U.S.A.), dialysed against six changes of distilled water over two days and lyophilised.

The material used in skin testing was prepared at 1 mg ml^{-1} in 50% Coca's solution: 50% glycerol, and passed through a 0.45μ Millipore filter into a glass bottle with plastic cap and applicator (Bencard Ltd, Worthing, England). Histamine at 1 mg ml^{-1} was used as a positive control solution and 50% Coca's solution: 50% glycerol as a negative control.

Crude *Ch. riparius* (CTT) total haemoglobin sent by Dr. X. Baur, had been extracted from larvae following the technique of Baur *et al.* (1982), and was prepared at 0.1 mg ml^{-1}.

(iii) *Preparation of allergenic fractions*. — Lyophilised *C. lewisi* extract, prepared according to the method outlined above, was applied in four separate batches of 200 mg to a Sephacryl S200 (Pharmacia, Uppsala, Sweden) column (90cm × 2.6 cm diameter, in 0.05M NH$_4$ HCO$_3$, at 29.5 ml
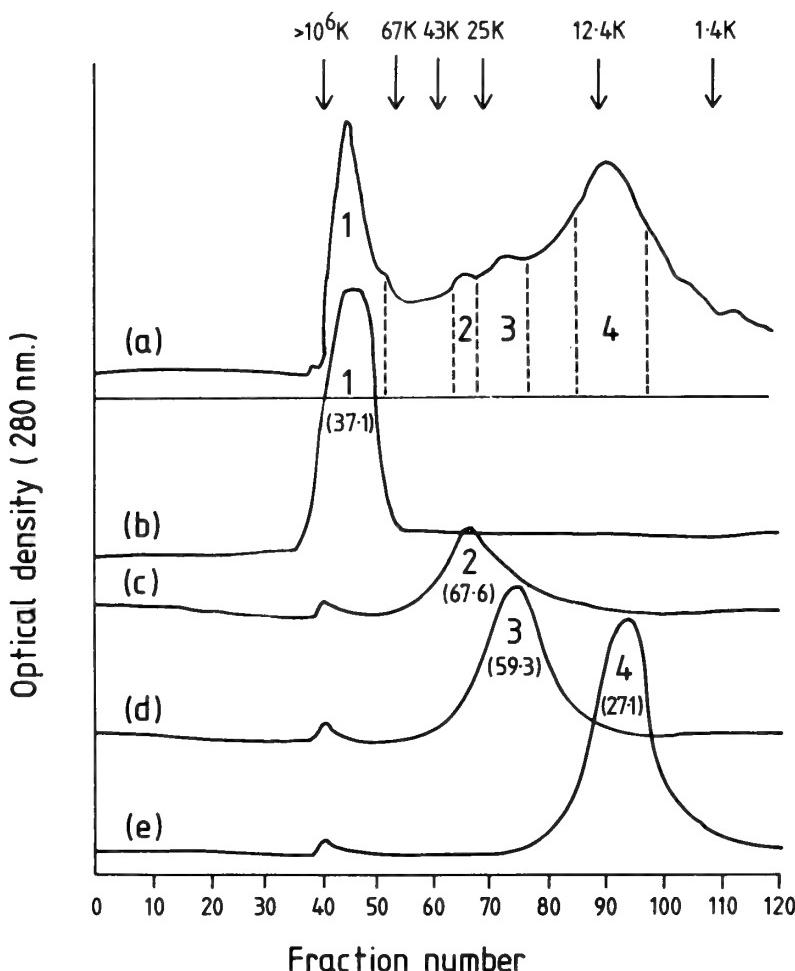
FIGURE 1.   Optical densities of *C. lewisi* extracts before and after rechromatography of fractions: a) 200 mg of unfractionated *C. lewisi* extract; (b), (c), (d) & (e) rechromatography of fractions 1, 2, 3 & 4 respectively from four fractionations of (a). Numbers in parentheses show relative magnitude of skin test weal response as indicated in the text. [Sephacryl S200 gel filtration, column calibrated with markers of known molecular weight from 1.4K to 10^6 daltons.]

Hr^{-1}). The column was calibrated with blue dextran ($> 10^6$K), bovine serum albumin (67K), ovalbumin (43K), chymotrypsin (25K), cytochrome C (12.4K) and vitamin B12 (1.4K). Four fraction areas were identified by O.D. profile at 280 nm (Fig. 1a), which demonstrated that Sephacryl S200 gave better resolution than Sephadex G100. The Kav of the two median fraction peaks (O.D. at 280 nm) (labelled 2 and 3 in Fig. 1) were 0.307 and
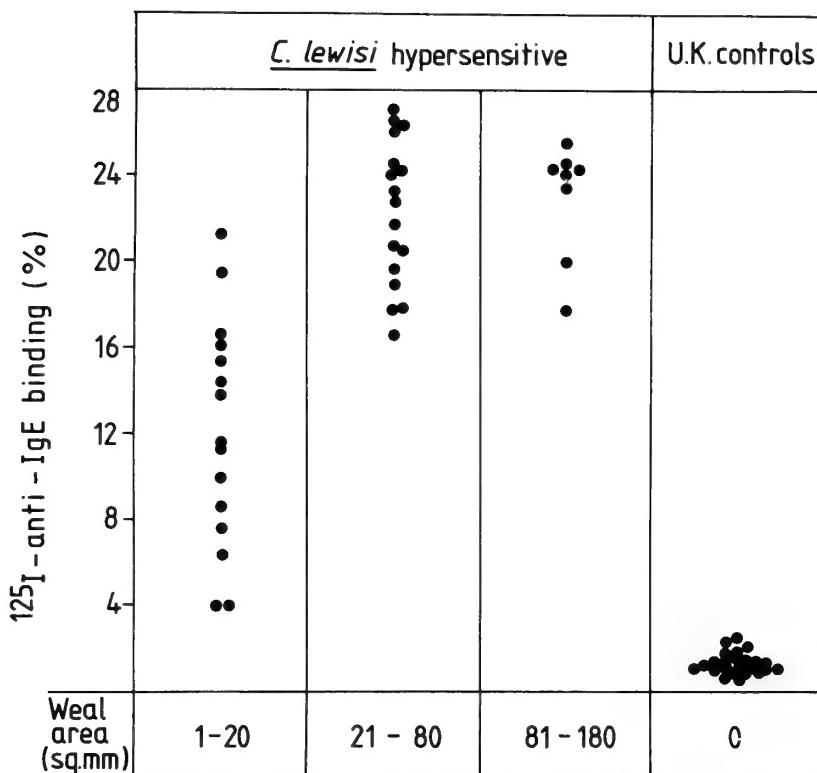
FIGURE 2.   Comparison of RAST and skin test weal response to *C. lewisi*. A control skin test with Coca's solution was performed at the same time as the *C. lewisi* skin tests. Any resultant weal 'area' was deducted from that produced by the test extract.

0.418 respectively, equivalent to molecular weights of approximately 32,000 and 17,000 daltons. Each of the four fraction areas from each of the four fractionations of extract were pooled individually and purified further by rechromatography on the S200 column as shown in Fig. 1b, c, d, & e respectively. After harvesting, these four fractions were lyophilised and used for skin testing.

RESULTS

Radioallergosorbent test (RAST). — After establishing the optimum conditions for the maximal binding of IgE in the RAST, the percentage of ^{125}I-anti-IgE binding was determined for the serum of each of the 40 hypersensitive Sudanese and 24 United Kingdom controls. The relationship
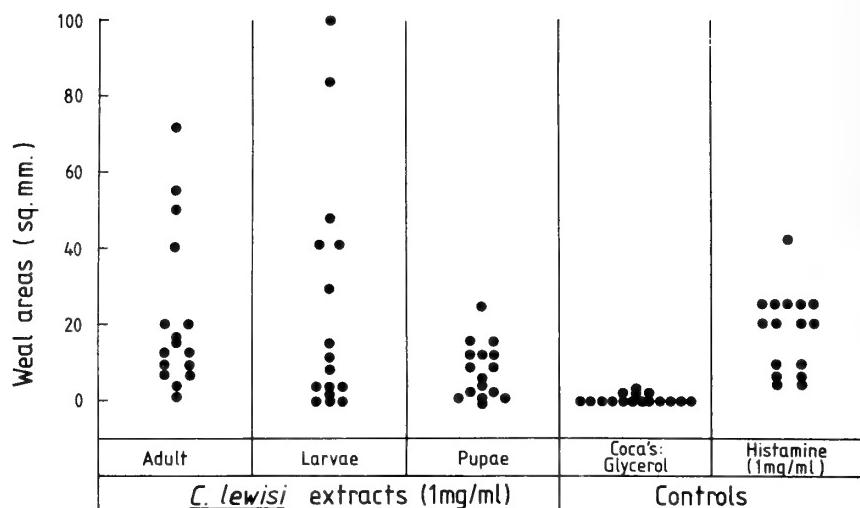
FIGURE 3.   Skin test weal response to adult, larval and pupal extracts of *C. lewisi*. Responses to the negative (Coca's solution) and positive (histamine) controls are shown.

between this percentage of isotope binding and the skin test reactivity of each individual, with the skin test response aggregated into three size categories, is illustrated in Figure 2. Twenty-four United Kingdom skin test negative controls gave between 0.6 and 2.6% isotope binding. Fifteen skin test reactive Sudanese with weal 'areas' (maximum × minimum weal diameters) of 1 - 20 mm^2 gave RAST values from 4 to 21% binding, and patients with stronger skin test responses of 21 - 80 m^2 had RAST values of between 17 and 27% binding. Eight individuals with very strong skin test reactions from 81 to 180 mm^2 did not give RAST values higher than those individuals giving intermediate (21 - 80 mm^2) size weals. All values were statistically highly significant: 1 - 20 mm^2 weals versus 0 mm^2 weals ($p < 0.005$), 1-20 mm^2 weals versus 21-80 mm^2 weals ($p < 0.025$), 21 - 80 mm^2 weals versus 81 - 180 mm^2 weals (not significant).

Skin 'prick tests. — The skin 'prick' test responses, as weal 'areas' of each of 16 Sudanese patients in the group tested with adult, pupal and larval extracts of *C. lewisi,* Coca's glycerol negative control and histamine positive control, are illustrated in Figure 3.

The skin test responses, as weal 'areas', of the other group of 26 Sudanese patients tested with the four rechromatographed S200 fractions of *C. lewisi* are shown in Figure 4, and the responses of the same individuals to four extracts of *Ch. riparius* (= CTT) are shown in Figure 5. The responses of these 26 individuals to the Coca's glycerol negative control and to the

histamine positive control were similar to those of the 16 patients of the first group shown in Figure 3. The range of responses to the negative control is shown in Figure 5, but omitted entirely from Figure 4. Each skin 'prick' response to these eight antigens (as measured in 26 patients) was standardised by conversion to a proportion of the response to unfractionated *C. lewisi* adult extract. In order to investigate possible differences between responses to antigens tested, a Fisher-Yates analysis of variance test was applied to these data. The results, ranked from high to low response, are as follows: The response to allergen fraction 2 is significantly greater than to allergen fraction 3 ($p < 0.0001$), which is significantly greater ($p < 0.0001$) than to *Ch. riparius* adult, laboratory and commercial larval extracts, none of which differ significantly from each other. *Ch. riparius* responses are significantly greater than to the high molecular weight allergen fraction 1 ($p < 0.005$). The response to the low molecular weight fraction 4 is significantly lower than to any other allergen tested ($p < 0.0001$).

In another analysis the weal data from *C. lewisi* extract and the four rechromatographed S200 allergen fractions were ranked and mean 'scores' rescaled to a mean value of 50. The Fisher-Yates analysis was applied where, with rescaled data, a difference of 10 is significant at the 0.1% level. The 'score' for unfractionated *C. lewisi* was 62.3, and the scores for S200 rechromatographed fractions 1, 2, 3, & 4 (Fig. 1) were 37.1, 67.6, 59.3 and 27.1 respectively (shown in Fig. 1 in parentheses under each peak).

Thus the response to fraction area 2 is significantly greater than to unfractionated *C. lewisi* and fraction area 3 ($p < 0.005$), which are significantly greater than to the high molecular weight fraction 1 ($p < 0.0001$), which in turn is significantly greater than to the molecular weight fraction 4 ($p < 0.0001$).

DISCUSSION

The responses of Sudanese individuals hypersensitive to *C. lewisi,* when tested with ten different chironomid antigenic extracts, give a strong indication that haemoglobins are major allergens in chironomid allergy in the Sudan. The four rechromatographed antigenic fractions elicited different responses which help to elucidate the nature of these allergens. The allergen area 2, with a molecular weight of approximately 32,000 daltons, elicited a significantly greater response than did the unfractionated extract. The allergen area 3, equivalent to a molecular weight of about 17,000, provoked a response equivalent to that of the unfractionated extract. The major allergenic activity is clearly associated with these two fractions. The higher molecular weight fraction 1 (molecular weight 66,000 and above) and the lower molecular weight fraction each elicited smaller responses, none higher
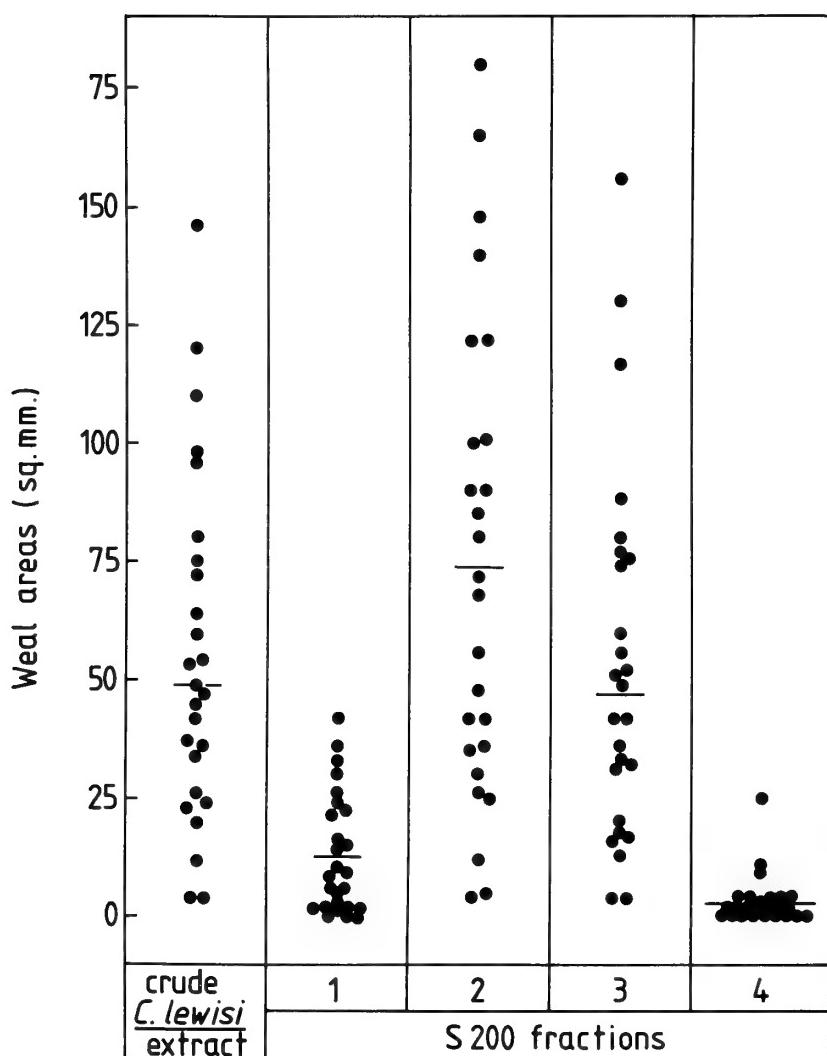
FIGURE 4.   Skin test weal response to 'crude' (unfractionated) and four rechromatographed fractions (Fig. 1 b, c, d & e) of *C. lewisi*. Any response to negative (Coca's solution) control is deducted.

than the response to unfractionated extract. However, in some individuals, there were weak but positive responses, particularly to the higher molecular weight fraction. Although the precise natures of fractions 2 and 3 are not fully elucidated, it is significant that the molecular weights of these fractions coincide quite closely with those reported for dimeric and monomeric
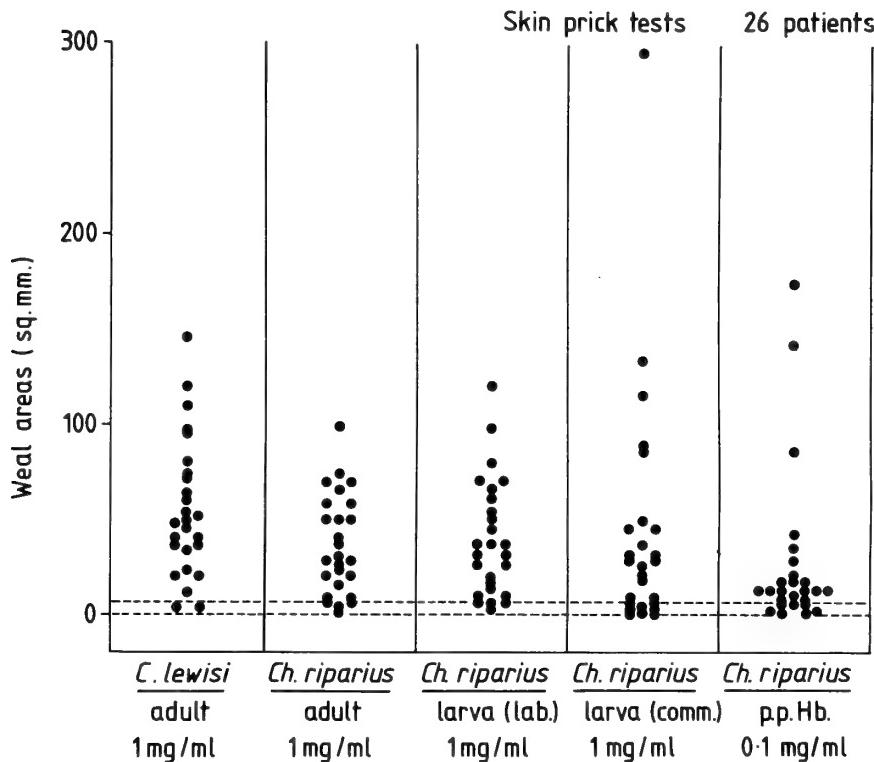
FIGURE 5.   Skin test weal responses to unfractionated *C. lewisi* and extracts from *Ch. riparius*. Abbreviations: lab.-laboratory culture; comm.-commercial, "Gamma Foods"; pp. Hb.-partially purified total haemoglobin (from Baur). Note: Haemoglobin is 1/10 dilution of other extracts. The interrupted lines delimit the range of responses to the Coca's negative control.

haemoglobins. The high molecular weight fraction contains some molecules with a molecular weight similar to that of tetrameric haemoglobin. Biochemical studies by Tee *et al.* (1983, in press) on the structure of the allergens are not in conflict with this identification.

Further indications that haemoglobins are major antigens in the *C. lewisi* allergy come from skin tests performed with extracts of *Ch. riparius* and of the immature stages of *C. lewisi*. *Ch. riparius* has been shown to contain potent allergens for people occupationally exposed to freeze dried larvae used by aquarists. The antigenic activity has been identified as belonging to specific peptide sequences within the different haemoglobins present in the haemolymph of the larvae, and apparently present also in the adult midges (Baur *et al.,* 1982). Our tests reported in this paper indicate that there is an

appreciable degree of cross-reactivity between the antigens of *Ch. riparius* and those of *C. lewisi,* evidenced by skin reactivity to extracts of both larval and adult *Ch. riparius.* Since *Ch. riparius* is a species unknown in the Afrotropical region and it is inconceivable that Sudanese sensitized to *C. lewisi* could have encountered *Ch. riparius* prior to skin testing, their skin test reactivity to *Ch. riparius* extracts is most likely to be due to the presence of similar antigens in these distantly related species. The presence of one or more antigens common to unrelated species of Chironomidae may be the explanation for the cross reactivity observed between subdominant species of Nilotic Chironomidae reported by Cranston *et al.* (in press). That these antigens include haemoglobins is confirmed by the response of *C. lewisi* sensitised Sudanese to tests with the *Ch. riparius* haemoglobin supplied by Dr. X. Baur. Although this antigen was prepared at 1/10 the dilution of all others tested, a strong positive response was elicited in several of the patients tested, and weaker responses in many others.

Since the occupational sensitisation reported by Baur was to antigens shown to be present in larval Chironomidae, it was important to test whether the immature stages of *C. lewisi* were antigenic. That numerous individuals did show reactivity to extracts of larvae, and to a lesser extent to the pupae, can be explained most parsimoniously as being due to the presence of similar antigens in all stages of this holometabolous insect. This conclusion is strengthened by Baur's (1982) discovery that both larvae and adults of *Ch. riparius* contain similar antigenic determinants, namely haemoglobins.

Further evidence for the close similarity between the antigens present in *Ch. riparius* and *C. lewisi* comes from RAST tests. Baur (1982) reported that the sera of *C. lewisi* sensitised patients contained high titres of *Ch. riparius* haemoglobin specific antibodies. Conversely, the serum of one *Ch. riparius* sensitised individual contained antibodies specific to extract of *C. lewisi.* However, Tee (R.D. Tee, *unpubl. obs.*) found that there was variable inhibition of the *C. lewisi* RAST by *Ch. riparius* total haemoglobin provided by Baur, indicating that although haemoglobins are clearly significant in the problem, they may not account for the total allergenicity in all *C. lewisi* sensitive individuals. The considerable amount of variability between individual responses to skin tests may similarly indicate that the antigens of *C. lewisi* may not be completely identical to those of *Ch. riparius.* Whether one would expect total inhibition of the RAST by haemoglobins from distantly related species of Chironomidae is an open question. Although high immunological cross-reactivity between haemoglobins of different species of *Chironomus* was demonstrated by Baur *et al.* (1982) and Tichy *et al.* (1982), the species examined belong to the same genus, while *C. lewisi*

and *Ch. riparius* are in different tribes, although belonging to the same sub-family.

If, as seems likely, chironomid haemoglobins are important allergens in the Sudanese midge allergy, as in the *Ch. riparius* occupational allergy, questions remain unanswered concerning the mechanism by which the haemoglobin is available as a rapid acting allergen associated with adult *C. lewisi*. Susceptible Sudanese individuals may have an asthma attack triggered by contact with a single midge and the onset of the attack may be immediately on contact with the whole fly. The limited amount of information available, based on studies of one or two species of the genus *Chironomus,* suggests that the larval haemoglobin which is present in the haemolymph of many Chironomidae, may not be fully broken down during metamorphosis, but may persist in the pupa and, to a lesser extent, in the adult (Schin *et al.,* 1974). Laufer & Poluhowich (1971), studying *Chironomus pallidivittatus,* showed that haemoglobin, and what appeared to be breakdown products of haemoglobin metabolism, were present in the meconium of the newly emerged adult midge. Further investigations are required to establish whether haemoglobins and related antigenic molecules are present in the meconia of the newly emerged (and short-lived) adult *C. lewisi* and whether this might be a significant mechanism for the dispersal of the antigens.

Although haemoglobins are believed to be present in many Chironomidae, particularly in the subfamilies Chironominae and Tanypodinae, precise information on the distribution within the family is missing. Detailed understanding of the structure of chironomid haemoglobins is restricted almost entirely to the genus *Chironomus.* The inadequacy of our knowledge concerning the importance and prevalence of these antigenic molecules restricts our ability to speculate on the extent of the problem of chironomid allergy. However, in reporting their findings on the cross-reactivity between *Ch. riparius* and *C. lewisi,* Baur and his colleagues (1982) suggest that "the increase in asthmatic diseases reported by several authors in water-rich regions such as river basins during the chironomid season is predominantly caused by sensitisation to haemoglobin molecules in this insect family." Our investigations tend to support this suggestion, and, in view of our field-based studies, indicate the potentially world-wide nature of this environmental allergen. We have suggested that the environmental conditions which allow the development of huge populations of adult midges along the River Nile are not unique to this region. Indeed, Ali (1980), in documenting nuisance midge outbreaks and their control, lists eight countries which have been afflicted with midge outbreaks serious enough to have been documented in the literature. Our own obser-

vations, together with those of colleagues studying chironomids, show that problems of nuisance chironomids are steadily increasing as waters become more eutrophic, and man lives closer to such habitats. Ali reviews in some detail the midge nuisance in central Florida, and now, for the first time, there is evidence (through responses to skin 'prick' test) that some inhabitants of this region have become hypersensitive to chironomid midges (Cranston, *unpubl. obs.*).

In view of these findings, chironomids must be seen as more than a source of world-wide nuisance causing economic problems through the defacing of buildings and paintwork, traffic hazards and restriction of outdoor activity, but should be seen as significant environmental allergens.

REFERENCES

ALI, A. 1980. Nuisance Chironomids and Their Control: a Review. Bull. ent. Soc. Am. 26:3-16.

BAUR, X. 1982. Chironomid hemoglobin — a major allergen for humans. Chironomus 2(3):24-25

BAUR, X., M. DEWAIR, G. FRUHMANN, H. ASCHAUER, J. PFLETSCHINGER, AND G. BRAUNITZER, G. 1982. Hypersensitivity to chironomids (non-biting midges): localisation of the antigenic determinants within certain polypeptide sequences of hemoglobins (erythrocruorins) of *Chironomus thummi thummi* (Diptera). J. Allergy Clin. Immunol. 68;66-76.

BROWN, A.W.A., D.J. McKINLEY, H.W. BEDFORD AND M. QUTUBUDDIN. 1961. Insecticidal operations against chironomid midges along the Blue Nile. Bull. ent. Res. 51:789-801.

CRANSTON, P.S., M.O. GAD EL RAB AND A.B. KAY. 1981. Chironomid midges as a cause of allergy in the Sudan. Trans. R. Soc. trop. Med. Hyg. 75(1):1-4.

CRANSTON, P.S., R.D. TEE, M.O. GAD EL RAB AND A.B. KAY. (in press). Immediate-type skin reactivity to extracts of the 'green nimitti' midge, (*Cladotanytarsus lewisi*) and other chironomids in asthmatic subjects in the Sudan and Egypt. Ann. trop. Med. Parasit.

CREDLAND, P.F. 1973. The taxonomic status of *Chironomus riparius* Meigen and *Chironomus thummi* Kieffer (Diptera: Chironomidae). J. nat. Hist. 7:209-216.

FREEMAN, P. 1950. A species of Chironomid (Diptera) from the Sudan suspected of causing asthma. Proc. R. ent. Soc. Lond. (B) 19:58-59.

GAD EL RAB, M.O. AND A.B. KAY. 1980. Widespread immunoglobulin E-mediated hypersensitivity in the Sudan to the 'green nimitti' midge, *Cladotanytarsus lewisi* (Diptera: Chironomidae). I. Diagnosis by radioallergosorbent test (RAST). J. Allergy Clin. Immunol. 66(3):190-197.

GAD EL RAB, D.R. THATCHER AND A.B. KAY. 1980. Widespread IgE-mediated hypersensitivity in the Sudan to the 'green nimitti' midge, *Cladotanytarsus lewisi* (Diptera: Chironomidae). II. Identification of a major allergen. Clin. Exp. Immunol. 41;389-396.

KAY, A.B., M.O. GAD EL RAB, J. STEWART AND H.H. ERWA. 1980. Widespread IgE-mediated hypersensitivity in Northern Sudan to the chironomid *Cladotanytarsus lewisi* ("green nimitti"). Clin. Exp. Immunol. 34:106-110.

KAY, A.B., M.O. GAD EL RAB, P.S. CRANSTON, C.M.U. MACLEAN AND R.D. TEE. 1983 Clinical, Entomological and Epidemiological studies on Allergy to a Non-biting midge (*Cladotanytarsus lewisi*) (green nimitti). Clin. Allergy Suppl. Proc. XI Int. Congr. Allerg. & Clin. Immunol. pp. 463-467, Macmillan, Basingstoke 1983.

KAY, A.B., C.M.U. MACLEAN, A.H. WILKINSON AND M.O. GAD EL RAB. (in press). The prevalence of asthma and rhinitis in a Sudanese community seasonally exposed to a potent airborne allergen (the 'green nimitti' midge, *Cladotanytarsus lewisi*). J. Allergy Clin. Immunol.

KIRK, R. 1952. Report of Medical Services, Ministry of Health, Sudan Government [Khartoum]. 1950/1:44-45.

_____. 1953. Report of Medical Services, Ministry of Health, Sudan Government [Khartoum]. 1951/2:43.

LAUFER, H. AND J. POLUHOWICH. 1971. A factor controlling the concentration of hemoglobins of *Chironomus* during metamorphosis. Limnologica, Berlin 8:125-126.

LEWIS, D.J. 1956. Chironomidae as a pest in the Northern Sudan. Acta trop. 13:142-158.

_____. 1957. Observations on Chironomidae at Khartoum. Bull ent. Res. 48:155-184.

_____, A.J. HENRY AND D.N. GRINDLEY. 1954. Daily changes in the numbers of chironomid midges at Khartoum. Proc. R. ent. Soc. Lond. (A) 29:124-128.

SATTI, M.H. AND O.M. ABDEL NUR. 1974. Chironomidae as a cause of nuisance and allergic manifestation. Sudan med. J. 12:77-80.

SCHIN, K.S., J.J. POLUHOWICH, T. GAMO AND H. LAUFER. 1974. Degradation of haemoglobin in *Chironomus* during metamorphosis. J. Insect Physiol. 20:561-571.

TEE, R.D., M.O. GAD EL RAB, P.S. CRANSTON AND A.B. KAY. 1983. Allergens of the "green nimitti" midge. Clin. Allergy Suppl. Proc. XI Int. Congr. Allergy & Clin. Immunol. pp. 541-544. Macmillan, Basingstoke, 1983.

TEE, R.D., J.L. LONGBOTTOM, P.S. CRANSTON AND A.B. KAY. (in press). Partial characterisation of allergens associated with hypersensitibity to the "green nimitti" midge (*Cladotanytarsus lewisi*, Diptera: Chironomidae) Clin. Allergy.

TICHY H., T. KLEINSCHMIDT AND G. BRAUNITZER. 1981. Studies on the Evolutionary Relationships Between Hemoglobins in *Chironomus pallidivittatus* and *C. tentans*. I. Isolation and Immunological analysis of Monomeric and Dimeric Hemoglobins. J. mol. Evol. 18:9-14.

WIDE L., H. BENNICH AND S.G.O. JOHANSSON. 1967. Diagnosis of allergy by an *in-vitro* test for allergen antibodies. Lancet 2:1105.

WÜLKER, W. 1963. Prospects for biological control of pest Chironomidae in the Sudan. W.H.O./E.B.L. Series 11, Vector Control 42:1-23.

A Description of Two New species of Tanypodinae (Diptera: Chironomidae) from North Africa.

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ABSTRACT. — The male imagines of a new species of the Genera *Thienemannimyia* and *Rheopelopia* are described. The species were collected in North Africa. The pupal exuvium of the *Rheopelopia* species is known. The species are illustrated.

INTRODUCTION

The Tanypodinae of the *"Thienemannimyia* series" can be distinguished by the presence of a simple, but distinct lobe on the inner edge of the gonocoxite (Fittkau, 1962). Material collected in North Africa, which was made available to the author by Dr. E.J. Fittkau and Dr. F. Reiss, was found to contain a number of specimens from this series. A description of two new species from the collections is presented in this paper. The terminology used follows that of Saether (1980).

Thienemannimyia choumara sp.n.

Imago male (n = 3). Length 3.75-4.00 mm.
Head: AR 1.4-1.5: Antenna with 13 flagellomeres. Proximal end of last flagellomere darkened. Palpal segments pale, whitish-yellow. Clypeus dark yellow.
Thorax: Color yellow; scutal stripes mid-brown; Wing: — length 2.3 mm; membrane very pale, cross-vein RM and FCu with yellow markings. Legs, pale yellow with darker ring at tip of femora. Leg measurements as follows (μm):—

	Fe	Ti	Ta$_1$	Ta$_2$	Ta$_3$	Ta$_4$	Ta$_5$	LR
P$_1$		930-						
	820	970	680	360	—	—	—	0.7
P$_{11}$	830-	800-	430-	230-	200	150	100	0.2-0.3
	850	820	440	240	—	—	—	
P$_{111}$	78-	104-	—	—	—	—	—	—
	80	107	—	—	—	—	—	—

Abdomen: Color, pale yellow. Tergites II-VI with darker oral band consisting of a median and two lateral spots linked together. Tergite VII and VIII darker, VII with a pale μm, anal band.

89
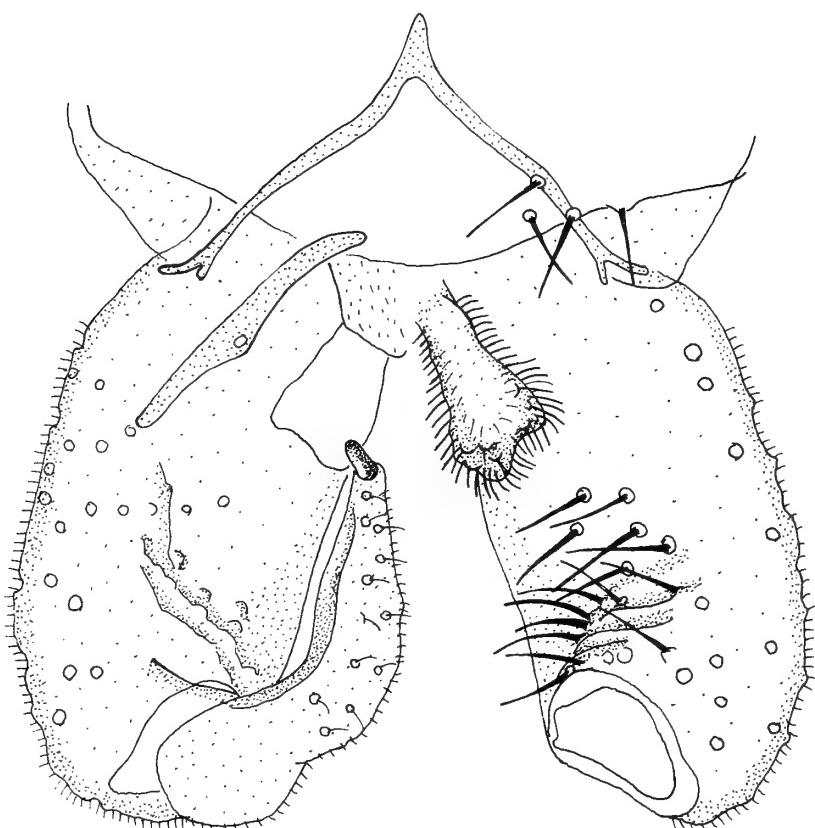
FIG. 1.   *Thienemannimyia choumara* sp. n. — male hypopygium.

Hypopygium: (Fig. 1). Gonocoxite 158 um, twice as long as broad. Gonostylus 115 μm, slightly curved. Gonocoxal lobe 56 um, approximately one third the length of gonocoxite.
Female imago, pupa and larva; Unknown.

Type locality: Morocco.
Holotype: 1 ♂ labelled "*Thienemannimyia choumara* sp. n. Morocco Sp. 1 M6." Leg. Choumara. Det. C. Dowling, 1982. Type mounted on microscopic slide deposited in Zoologische Sammlung des Bayerischen Staates, Munich.
Paratype: 1 ♂ labelled "*Thienemannimyia* Sp. 1. Morocco 1397 68u:1070 68 M7, *T. choumara*" Leg. Choumara. Det. C. Dowling, 1982. (1397.68 = Environs of Berkane, Monts Beni, Shassen, 1968. 1070.68 = Environs of Marrakesh, Souk des Judais, 1968. Two different samples, broken at
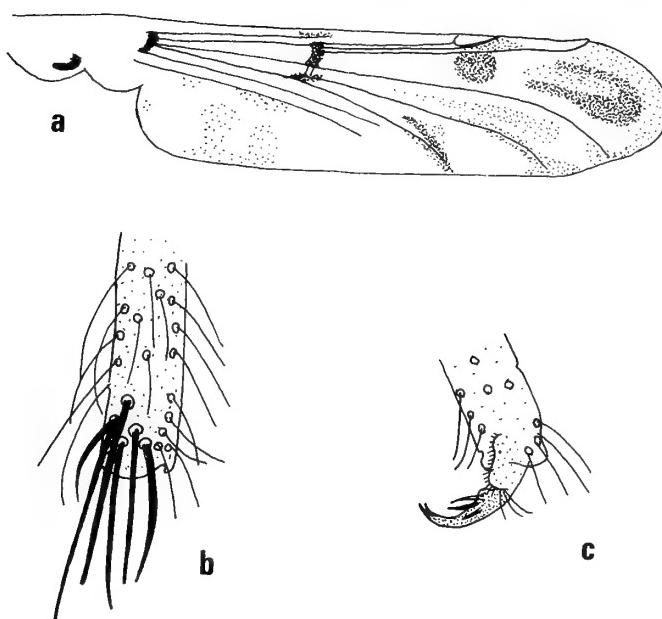
FIG. 2. *Rheopelopia murrayi* sp. n. (a) Male — wing. (b) Crown of setae on tip of tarsal segment 111, leg 11. (c) Claws and pulvilli.

transport and mixed — information supplied by Dr. F. Reiss). Mounted on microscopic slide deposited in Zoologische Sammlung des Bayerischen Staates, Munich.

Comments: Members of the Genus *Thienemannimyia* can be separated by the various markings on the wings and legs, as well as the structure of the male genitalia. On these criteria *T. choumara* sp. n. appears similar to *T. geijskesi* (Goetgh.), having no markings on the wing and a brown ring at the tips of the femora. *T. choumara* can be distinguished from *T. geijskesi* by darkened scutal stripes, smaller leg ratios and the structure of the genitalia. *T. tinctoria* (Freeman), the only other member of the Genus recorded from Africa (Freeman, 1955) can be differentiated by the presence of a brown ring on the base of the tibiae.

Rheopelopia murrayi sp. n.

Imago male (n = 2):   Length 4.0-4.5 mm.
Head: AR 1.50-1.55. Antenna with 13 flagellomeres, the proximal end of the last flagellomere darkened. Palpal segments, pale brown; Clypeus, pale brown.
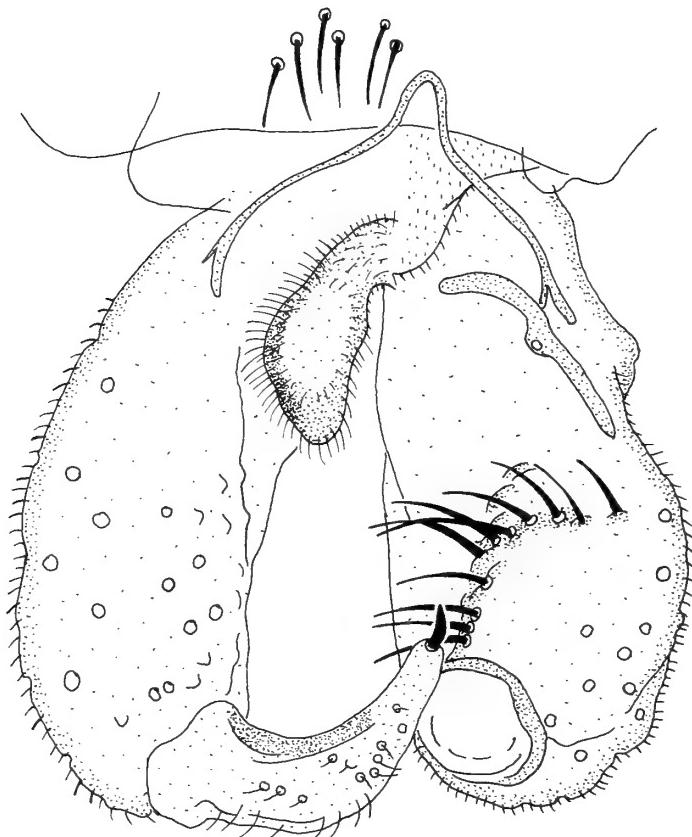
FIG. 3.   *Rheopelopia murrayi* sp. n. — male hypopygium.

Thorax: Color pale brown, scutal stripes mid-brown. Wing, length 2.5 mm, membrane pale with markings as in Fig. 2. Legs, pale yellow with ring at tips of the femora and paler ring at bases of the tibiae. Crown of setae on P_{11} Ta $_{111}$ (Fig. 2). Claws trifid; pulvilli present, less than half the length of the claw, but not clearly visible on all legs (Fig. 2).

	Fe	Ti	Ta_1	Ta_2	Ta_3	Ta_4	Ta_5	LR
P_1	900-950	1080	740	400	300	210	140	0.68
P_{11}						120-	110-	
	980	970	500	270	220	170	160	0.50
P_{111}	930	1210	780	410	320	220	140	0.64

Abdomen: Tergites II-VI pale, with darker oral band: VII and VIII completely brown.

Hypopygium: (Fig. 3). Gonocoxite 178.5 um, approximately half as long as wide. Gonostylus 127.5 μm, curved. Gonocoxal lobe 61 μm, just greater than one third gonocoxite length.
Female imago; Unknown.
Pupa. (n = 1). Color yellow. Length, Abdomen 4.5 mm. Cephalothorax 1.5 mm. Thoracic horn, similar to *R. ornata,* longer than the first abdominal segment. LS setae on abdominal segment VIII well developed, longer than the length of the segment. LS_1 situated on the middle of the segment edge. Anal lobe as long as broad. Anal lobe tooth slightly less than half the length of the lobe. Anal lobe setae longer than the lobe, the hind seta situated on the middle of the lobe edge.
Larva; Unknown.

Type locality: Morocco.
Holotype: 1 ♂ labelled "Morocco 2 354.67 M10. *Rheopelopia murrayi* sp. n. Tata, Moyen Dra. 1967". Leg. Choumara. Det. C. Dowling, 1982. Type mounted on microscopic slide deposited in Zoologische Sammlung des Bayerischen Staates, Munich. Tip of a second abdomen mounted beside the legs.
Paratype: 1 ♂ labelled "F 28A Sahara. Rearings from a small stream, Zousfana, Algerien 19.3.1955. *Rheopelopia murrayi*". This specimen was obviously dissected from the pupal exuvium also mounted on the slide. Mounted on microscopic slide deposited in Zoologische Sammlung des Bayerischen Staates, Munich. Leg. E.J. Fittkau. Det. C. Dowling, 1982.
Comments: The relationship of *Rheopelopia murrayi* sp. n. with other members of the Genus is difficult to determine. The pupal features would suggest that it belongs to the "ornata-group" (Fittkau, 1962). In fact on the basis of the characters listed, it is difficult to separate the pupa from that of *R. ornata* (Meig.). On the specimen examined, the thoracic horn is bent, but it appears to be somewhat longer and narrower than that of examined specimens of *R. ornata*. The adult characteristics suggest that *R. murrayi* is closer to *R. eximia* of the "maculipennis-group". The pulvilli are present but they are small and are not clearly visible. *R. eximia* is the only other species with a brown ring at the base of the tibiae. The long oval shape of the gonocoxal lobe in *R. murrayi* is clearly different from that of other European species.

References

FITTKAU, E.J. 1962. Die Tanypodinae (Diptera, Chironomidae). Die Tribus Anatopyni, Macropelopinii und Pentaneurini)-Abh. Larvalsystem Insekten: 1-453.

FREEMAN, P. 1955. A Study of African Chironomidae. Part 1. Bull. Br. Mus. Nat. Hist. (Entomology) 4(1):1-67.

SAETHER, O.A. 1980. Glossary of Chironomid morphology terminology (Diptera, Chironomidae). Ent. Scand. Suppl. No. 14. 51 pages.

Morphological and Ecological Remarks on the Larva of

Chernovskiia macrocera (Chernovskii)

(Diptera: Chironomidae)

By

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ABSTRACT. — The larva of *Chernovskiia macrocera* (Chernovskii) is redescribed on the basis of specimens collected in the Po River (northern Italy) and its ecology is reported. An overall agreement with Chernovskii's description is established and certain differences are discussed.

Since 1974 the National Electricity Board of Italy has carried out a biological survey to determine the effects of the nuclear power plant at Caorso (northern Italy) on the aquatic environment of the Po River. During this survey, several groups of macroinvertebrates living on the macrophytes of the riverside or on the sandy bed of the central part of the river, were investigated from a systematic standpoint. Among these groups the chironomids played an important role, by having the greatest number of species. Several of these chironomids were previously unknown in Italy.

The occurrence of *Robackia demeijerei* (Kruseman), *Beckidia zabolotskyi* (Goetghbuer), and *Chernovskiia macrocera* (Chernovskii) was somewhat of a surprise.

The occurrence of *Chernovskiia macrocera* is of particular interest. Since Chernovskii's first description of larvae from the River Volga, I believe no further specimens have been collected. The extreme rarity of this species is also demonstrated by the fact that only 5 of approximately 50,000 chironomids that I examined were *Chernovskiia macrocera*.

The larvae I collected corresponded in their measurements and in almost all morphological details with Chernovskii's description (1949) (Fig. 1). In my specimens the number of antennal segments varied from 7 (Fig. 2) to 8 (Fig. 3), while Chernovskii speaks only of 8 segments (Fig. 1). Although this might demonstrate a difference between the two descriptions, this is not necessarily so. In Chernovskii's description the first antennal segment is divided into two parts. Thus, his 8 antennal segments result from counting each of these division as a segment. I found some specimens to have 7

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antennal segments, because the first segment (or the first division of this segment), is much less sclerotized than the rest of the segment and possibly retracted into the head in some way.

The following character should be added to Chernovskii's description: premandible with 4 teeth (Fig. 2, Pm). *Chernovskiia orbicus* has 3 pre-mandibular teeth.

The mentum (M) in my specimens also differs from Chernovskii's description. In my specimens (Fig. 2, 3, M) the anterior margin is deeply concave, with 1 median tooth and 5-6 pairs of flat, light brown, lateral teeth. On both sides of the mentum 2 lobes can be seen, with striae visible only with difficulty. These lobes probably represent the ventromental plates (Fig. 2, 3, VmP). Chernovskii did not note these lobes, and because of the lack of the ventromental plates, placed his larvae in the subfamily Orthocladiinae and provisionally named them Orthocladiinae gen. ? 1 *macrocera.*

Saether (1977) revised the *Harnischia* complex and erected the genus *Chernovskiia,* in which he included Chernovskii's larvae together with *C. orbicus* (Townes), although he hypothesized that they could represent the larval stage of *C. amphitrite* (Townes). Saether only had Chernovskii's drawings available, and it was natural for Saether to attempt to interpret what particulars of Chernovskii's drawings could be the ventromental plates. The first "true" larvae of *C. macrocera* that Saether could have examined were those collected by myself and forwarded to him by A.M. Nocentini at the end of 1981. Thus, Saether wrote (according to a personal communication with J.E. Sublette) that what appears to be the lateral teeth of the mentum, could in fact be " . . . the collapsed ventromental plates . . ." This is a very suggestive interpretation, but, on the basis of my observations, I believe it is not well-founded.

I feel that my observations have demonstrated that certain aspects of the larval morphology of *C. macrocera* and similar species are far from being completely clarified. I feel that further studies are necessary, perhaps using more refined microscopic techniques than those at my disposal.

The environmental characteristics of the collecting site correspond to those reported by Chernovskii. The larvae were collected from a sandy and muddy substrate in the central part of the Po River, some distance from either bank. At the collecting site at Metapotamal, the river is 9 m deep and about 400 m wide. During collecting visits the flow varied from 800 to 1800 m^3/sec. Oxygen concentrations remained at a reasonably high level

FIG. 1. *Chernovskiia macrocera* larva (after Chernovskii, 1949). (A) antenna. (CAS) caudal abdominal segments. (Hl) head, lateral view. (Hv) head, ventral view. (LS) labral sensillum. (M) mentum. (Md) mandible. (MP) maxillary palp.

Hv

Md

M

Hl

LS

CAS

MP

A
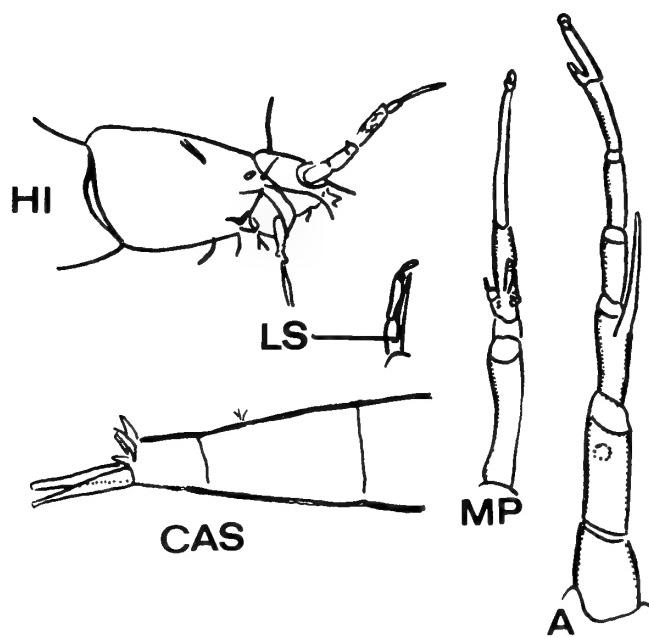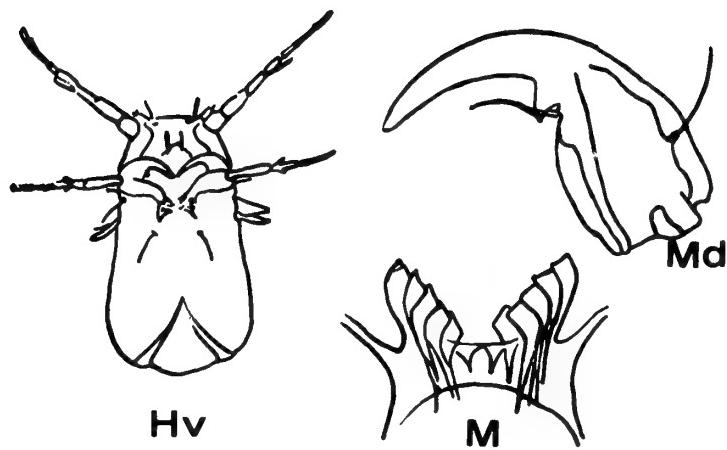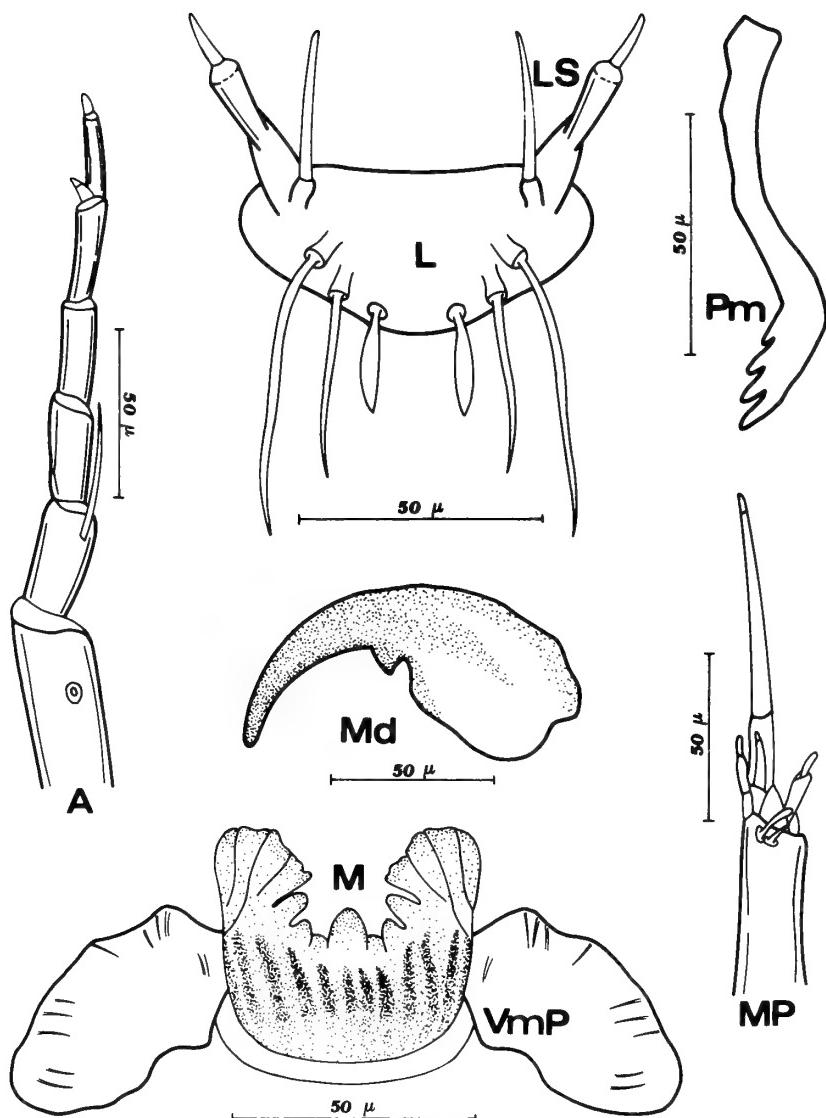
FIG. 2.   *Chernovskiia macrocera* larva from the River Po, with seven segmented antenna. (A) antenna. (L) labrum. (LS) labral sensilla. (M) mentum. (Md) mandible. (MP) maxillary palp. (Pm) premandible. (VmP) ventromental plates.
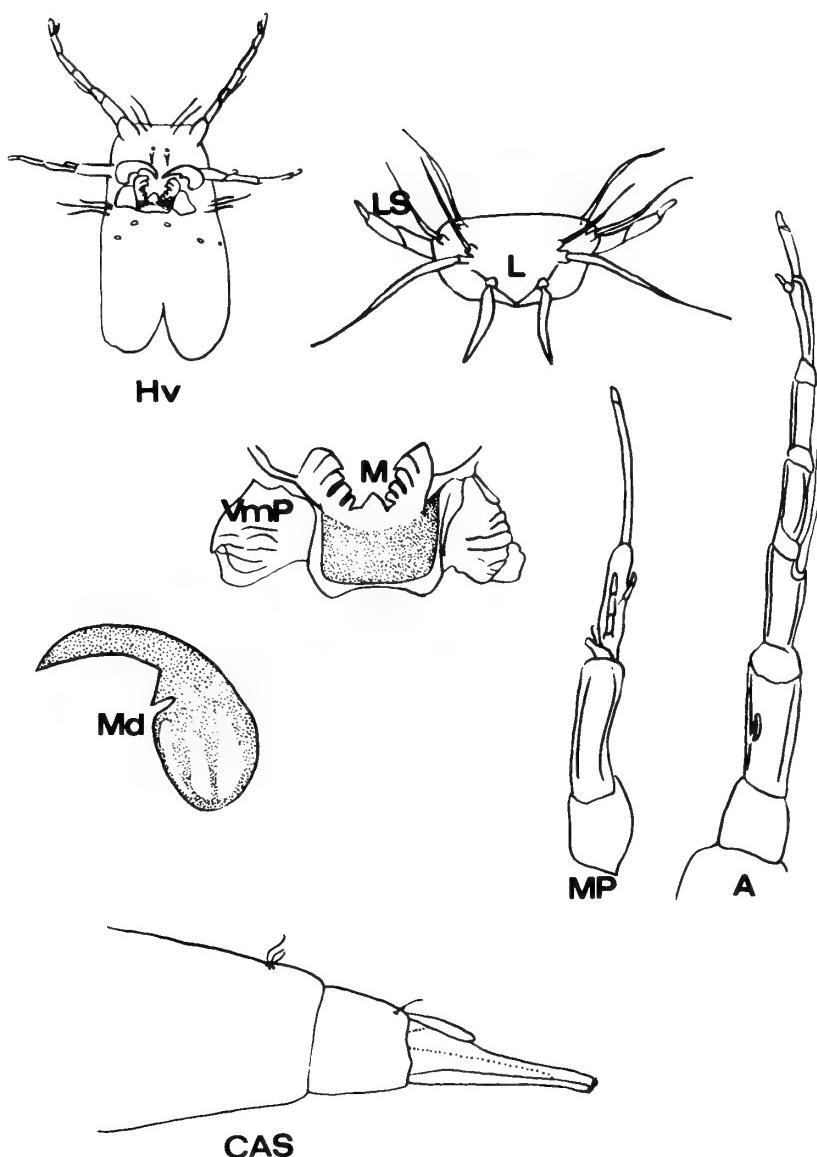
FIG. 3.   *Chernovskiia macrocera* larva from the River Po, with eight segmented antenna. (A) antenna. (CAS) caudal abdominal segments. (Hv) head, ventral view. (L) labrum. (LS) labral sensilla. (M) mentum. (Md) mandible. (MP) maxillary palp. (VmP) ventromental plates.

(7.3-10.5 ppm) and the other 45 chemical and physical values contributed to defining a mildly polluted environment. Cases of acute pollution were only occasionally verified. *Cheronovskiia macrocera* has not recently been found in other large West European rivers possibly because of their more serious pollution problems.

LITERATURE CITED

CHERNOVSKII, A.A. 1949. Opredelitel lichinok komarov semeistva Tendipedidae. Izd. Akad. Nauk, SSSR 31:1-186.

————. 1961. Identification of larvae of the midge family Tendipedidae. (Translation E. Lees, Editor K.E. Marshall). National Lending Libr. Sci. Tech., Boston Spa, Yorkshire. 300 pp.

SAETHER, O.A. 1977. Taxonomic studies on Chironomidae: *Nanocladius, Pseudochironomus,* and the *Harnischia* complex. Bull. Fish. Res. Bd. Canada 196:1-143.

Interdigitating Broadscale Distributional Patterns
of some Kansas Chironomidae

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ABSTRACT. — Preliminary investigations of the Chironomidae species occurring within the state of Kansas has revealed taxa which indicate the faunal composition of the state is influenced by species exhibiting six generalized distributional patterns. In addition to cosmopolitan species and eastern species with western distributional limits in the central plains, six species common to the southwest or to states west of the Rocky Mountains have been collected in western Kansas. Two species with more northerly or Rocky Mountain distributions have also been collected in western Kansas. Two species with more southerly or southwestern distributions are common to eastern and central Kansas. Six species common throughout the state are considered as having a central plains distribution. In addition a distinctive but subordinate Ozarkian Plateau influence is implicated. These statewide patterns of broadscale interdigitating distributions appear to be consistent with those found for other aquatic insect taxa inhabitating the state.

INTRODUCTION

In 1974 the staff of the State Biological Survey of Kansas initiated a long term study of the organisms occurring in aquatic environments of the state of Kansas. The stated goals of this study are to determine on a county-by-county basis the species composition of aquatic invertebrates and to characterize the statewide distribution, abundance and populational nature of these organisms. The results of this ongoing project have been and will continue to be disseminated in an annual publications series entitled "Technical Publications of the State Biological Survey of Kansas," copies of which are available upon request.

Early in this study it has become evident that major distributional breakpoints for certain aquatic taxa occur within the political boundaries of Kansas (Coler and Slater, 1982; Gelhaus, 1982; Gilbert, 1980, 1979; Hamilton and Shuster, 1980, 1979; Huggins, 1981, 1978; Liechti, 1982, 1981, 1980, 1979, 1978; Liechti and Huggins, 1977; May, 1982a, 1982b; Shuster and Hamilton, 1978; Slater, 1982, 1981, 1980, 1979; Stewart and Huggins, 1977). A very distinctive east-west distributional demarcation is evidenced

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by certain species, particularly of the orders Hemiptera, Coleoptera, Ephemeroptera, and Plecoptera. Within these orders the westernmost distributional limits of more easterly distributed taxa are roughly coincident with the westernmost extensions of Oak-Hickory deciduous forests in eastern Kansas. In addition, the easternmost boundaries of several western or southwestern taxa appear to be roughly coincident with the easternmost edge of the high plains in western Kansas. For Odonata there also exists a north-south demarcation within the central plains states for species that have approximate east-west transcontinental distributions (Huggins, 1978).

In August of 1980 I became affiliated with the State Biological Survey and began to determine the species of Chironomidae collected within the state. At that time I felt that the chironomid fauna of the state would be composed principally of taxa that are cosmopolitan in their distribution, along with a lesser number of taxa of more easterly distribution which reach their westernmost distributional limits in the Great Plains. Owing to the predominance of major river courses with shifting sand substrates within the region, it was felt that numerous taxa associated with this substrate type, primarily "*Harnischia* Complex" species, would also be commonly encountered. The intent of this paper, however, is to discuss recently published (Ferrington, 1981, 1982) and as yet unpublished data which suggest that some broadscale interdigitating of distributional patterns similar to the type found for other aquatic insect orders also occurs with the Chironomidae. Preliminary distributional data are presented and potential geographic areas of influence are proposed based upon comparisons with existing known species distributions.

Methods

Light trap samples of Chironomidae in the collection of the State Biological Survey were the principal source of material for this paper. These samples were taken throughout the state and include collections from springs, small to large rivers, reservoirs and farm ponds. The geographic location and ecophysiographic regions of the state are indicated in figures 1a and 1b, respectively. Figure 2 illustrates the major rivers and county boundaries.

All identifications of species in this paper were based upon determinations of adult male specimens. Keys used for identification were Malloch (1915), Townes (1945), Roback (1971), Hansen and Cook (1976), and Oliver (1981). Original descriptions by Saether (1971) and Sublette (1960)
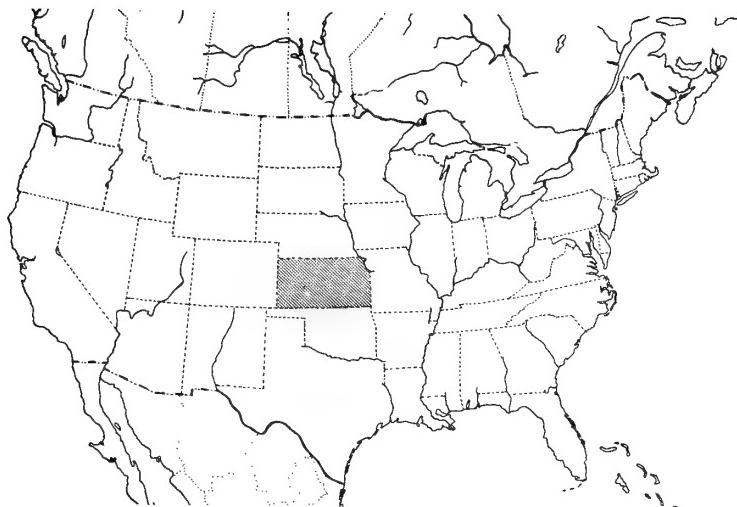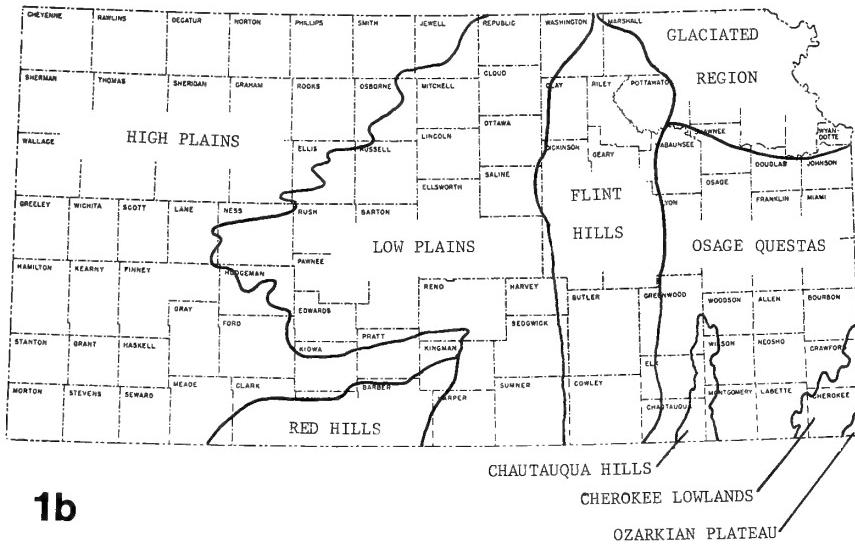
FIG. 1. Geographic location (1a) and ecophysiographic regions (1b) of Kansas.
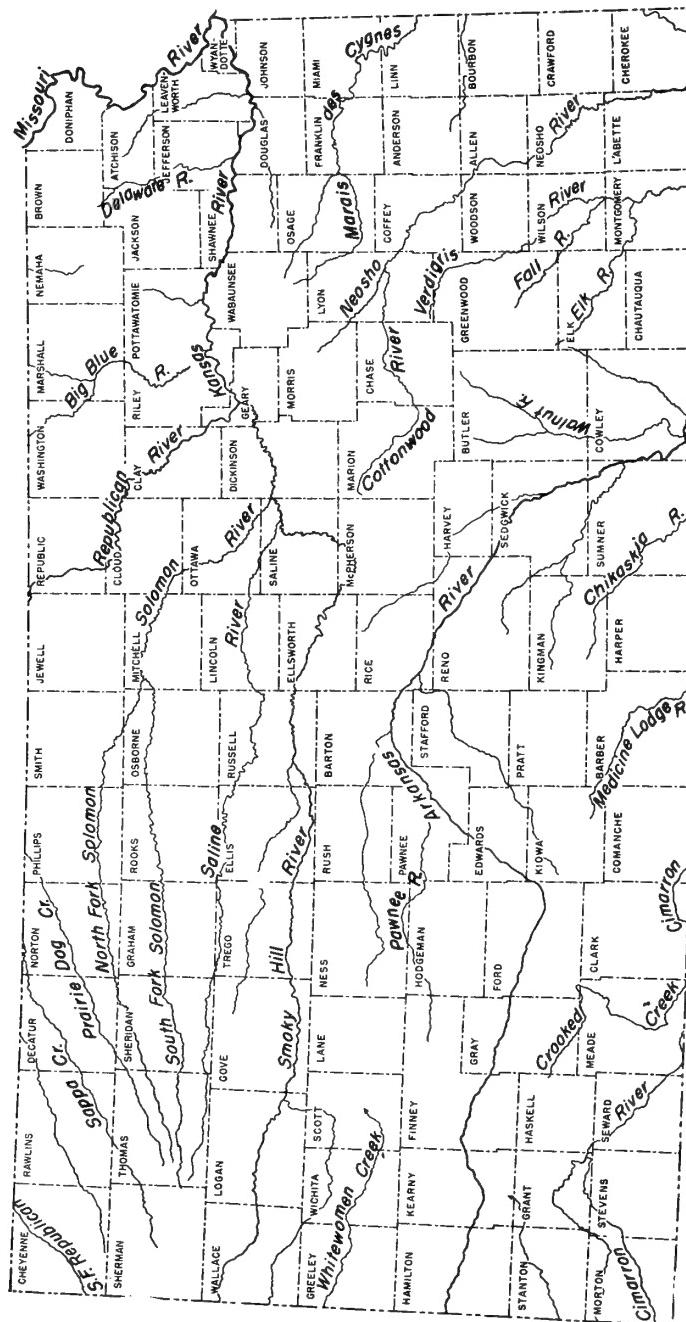
Fig. 2.   County boundaries and major rivers within Kansas.

were consulted for determinations of *Lenziella cruscula* and *Cryptotendipes ariel* respectively. Specimens of all species herein included are deposited in the collection of the State Biological Survey of Kansas.

RESULTS

As is the case with certain other aquatic insects, there appears to be four principal geographic influences contributing to the species richness of Kansas Chironomidae. The principal influences can be defined in general terms as east-west and north-south. In addition subordinate Ozarkian Plateau and Central Plains influences are also implicated. Species arranged according to geographic areas of influence are presented in tables 1-4.

Western or Southwestern Elements — The most surprising species records for the state have been those for species that were previously considered to occur only in the southwest or to be limited to the western side of the Rockies. These species are given in table 1. Ferrington (1981) previously reported the occurrence of *Thienemannimyia barberi* (Coquillett) and *Tanypus grodhausi* Sublette from collection sites along the South Fork of the Republican River near St. Francis in Cheyenne Co. Subsequent collections of *T. barberi* from the Arkansas River in Hamilton and Barton counties indicate that this species is widespread in the western half of the state, apparently being common to the high plains ecophysiographic region. *Cryptotendipes ariel* (Sublette) has also recently been collected from the South Fork of the Republican River at a site where *T. barberi* and *T. grodhausi* occur. *Paralauterborniella subcinctum* (Townes) and *Polypedilum isocerus* Townes also occur in counties within the high plains ecophysiographic region. *Stictochironomus naevus* (Mitchell) was collected from the inlet stream at Coldwater Lake in Comanche County, along the northern edge of Red Hills ecophysiographic region. All of these records represent the easternmost known occurrences of the species.

Northern Elements — This category contains two species within it, *Ablabesmyia pulchripennis* (Lundbeck) and *Diamesa heteropus* (Coquillett), see table 2. Distributional records for *A. pulchripennis* (see Roback, 1971) indicate that it is common across the Canadian shield region, extending from Alberta north to Greenland. To the south it has been recorded from Rocky Mountain areas in Colorado and Washington and from two miles north of Spearfish in the Black Hills region of South Dakota. The Hamilton County record in western Kansas is the southernmost record for this species.

TABLE 1. Chironomidae occurring in Kansas with known distributions primarily west of the Rocky Mountains or southwestern United States.

Taxon	Known distribution	Kansas Records
Thienemannimyia barberi	Arizona, California, Nevada, Utah, Washington	Cheyenne Co., Barton Co., Hamilton Co.
Tanypus grodhausi	California	Cheyenne Co.
Cryptotendipes ariel	California	Cheyenne Co.
Stictochironomus naevus	California, New Mexico	Comanche Co.
Paralauterborniella subcinctum	Nevada, California, New Mexico, Arizona	Wallace Co.
Polypedilum isocerus	Nevada, California	Scott Co.

TABLE 2. Chironomidae occurring in Kansas with known distributions primarily of a northern or northern Rocky Mountain nature.

Taxon	Known distribution	Kansas Records
Ablabesmyia pulchripennis	Greenland, Manitoba, Alberta, Quebec, South Dakota, Colorado, Washington	Hamilton Co.
Diamesa heteropus	Alaska, Washington, California, British Columbia, Colorado, Idaho, Minnesota, Montana, Nebraska, Nevada, New Mexico, Utah, Wyoming.	Cheyenne Co.

Hansen and Cook (1976) indicate that *D. heteropus* is the Diamesinae species most commonly encountered in the western United States. It has been my experience that *D. heteropus* is quite ubiquitous in upper alpine streams of the Beartooth Plateau region of Wyoming. The known distributional range of this species extends from Alaska south to New Mexico along the Rockies, and east across the northern plains through Nebraska to Minnesota. The Kansas record is from the South Fork of the Republican River near St. Francis in Cheyenne Co.

Southern, Southeastern or Ozarkian Elements — Three species are assigned to this category, see table 3. *Coelotanypus atus* Roback is quite common and widespread in Kansas. Previous records for this species indicate that it occurs along the Texas-Louisiana coastal regions and south into Puerto Rico. However, a recent record by Parkin and Stahl (1981) of two specimens collected in Illinois, combined with Kansas records, suggests that this species may be much more widespread in the southern and central plains states.

TABLE 3. Chironomidae occurring in Kansas with known distributions primarily of a southern, southeastern or possibly Ozarkian nature.

Taxon	Known distribution	Kansas Records
Coelotanypus atus	Louisiana, Texas, Puerto Rico	Widespread
Tanypus neopunctipennis	Bahamas, Mexico, Arizona, Florida, Illinois, Iowa, Louisiana, Missouri, Nebraska, Oklahoma, Tennessee, Texas	Widespread
Sympotthastia sp.	not known	Cherokee Co.

Roback (1971) provides a distributional map for *Tanypus neopunctipennis* Sublette. This species is very common in the southcentral and southeastern United States, with marginal populations extending west to New Mexico and Colorado and north to South Dakota. It is commonly collected by light trapping at the larger reservoirs within Kansas.

In contrast to *C. atus* and *T. neopunctipennis,* which are known to be more widely distributed to the south and/or southeast of Kansas, the occurrence of a species of *Sympotthastia* in Shoal Creek, Cherokee County is probably related to an Ozarkian Plateau influence. Shoal Creek originates in southwestern Missouri, flows northwest into Kansas and confluences with the Spring River south of Riverton, Kansas, less than six river miles west of the Kansas-Missouri border.

The occurrence of *Sympotthastia* in Kansas was rather surprising. The genus has not been recorded with any regularity in the North American literature, and immatures are poorly known (Simpson and Bode, 1980). Limited ecological data suggests that species of this genus occur in swift current areas of pristine lotic habitats. Beck (1977) lists it as rheobiontic and saprophobic. All this evidence leads me to conclude that this species may be restricted in the central states region to the area of the Ozarkian Plateau in Missouri and Arkansas and surrounding streams in which appropriate habitat areas occur. Thus, it would not be expected to occur in Louisiana, Mississippi or other states to the southeast or south of Kansas.

I initially became aware of the presence of this species in Kansas through the collection of a single pupa by Mr. Donald Huggins in January of 1981. Subsequent collections in February and March of 1982 by myself have indicated that the population density of this species is quite high during winter months in a section of Shoal Creek flowing through Schermerhorn Park south of Galena, Kansas. Several specimens have been reared and descriptions will be forthcoming. This is the southwestern most verifiable record for the genus.

Eastern Elements Or Widespread Species With Dense Populations In Central Plains Region — Table 4 lists species that show one of two types of geographic distributional patterns. These patterns are: (1) species common to the eastern United States and having their westernmost distributional limits in the Great Plains, or (2) species that are widespread in overall occurrence but which seem to have more dense populations in the Great Plains.

Species which are common in the eastern United States but have their westernmost distributional limits in the Great Plains are *Conchapelopia americana* (Fittkau) and *Diamesa nivoriunda* (Fitch). Records of rearings for *C. americana* by Roback (1981) indicate that this species occurs from New Hampshire to Florida along the east coast. In Kansas this species has been collected from two spring fed Flint Hills streams. Though not collected to date, it probably occurs in similar spring fed streams in the Osage Cuestas and Glaciated ecophysiographic regions of eastern Kansas. It is unlikely, however, that appropriate habitat exists for this species further west; the Flint Hills records thus probably represent its western distributional limit in Kansas.

Hansen and Cook (1976) state that *D. nivoriunda* is the most common northeastern species of *Diamesa*. This species is sometimes collected with *Diamesa cheimatophila* Hansen and Cook in the northeast and with *Diamesa mendotae* Muttkowski in midwestern states. The collection of *D. nivoriunda* in Bourbon County represents the southwestern most record for the species. It has been collected in Missouri, however, and the Kansas record thus represents only a small range extension. It is unlikely that this species occurs west of the Flint Hills. The occurrence of *D. nivoriunda* in Kansas, however, does suggest that *D. mendotae* could occur within the state. In view of the record of *Diamesa chiobates* Hansen and Cook in Osage County it would now seem not unlikely that there could potentially be four species of the genus that occur in Kansas.

The remaining species in table 4 are species that are known to be widespread in occurrence but are not reported with sufficient regularity to suggest that they comprise substantive populations. Within Kansas all of these species, with the exception of *D. chiobates,* are widespread and commonly encountered. This type of evidence thus tends to infer that the species are representative of a distinctive central plains element within the North American chironomid fauna.

The apparent rarity of *D. chiobates* in Kansas may simply be an artifact of collection efforts to date. As is the case with most *Diamesa,* this species was collected in early spring as an adult and is thus probably a late winter/ early spring emerging species. Additional early spring collections will be required to determine the commonness of this species in Kansas.

TABLE 4. Chironomidae occurring in Kansas that are common to the eastern United States, or species that are known to occur in only one or a few widely disjunct areas but appear to have dense populations within the central plains region.

Taxon	Known distribution	Kansas Records
Conchapelopia americana	Common in Eastern states including New Jersey, South Carolina, Pennsylvania, West Virginia, New Hampshire, Florida	Small prairie streams in Flint Hills
Diamesa nivoriunda	Alabama, Indiana, Massachusetts, Maryland, Michigan, Minnesota, Missouri, Newfoundland, New York, Ontario, Quebec, Virginia, Ohio, Pennsylvania, Wisconsin	Bourbon Co.
Tanypus nubifer	Manitoba, California, Kansas, Nebraska, Utah	Widespread
Tanypus concavus	Michigan, Iowa, New York, Texas, Virginia	Common
Paramerina smithae	California, South Dakota, Washington, Utah, Wyoming, Mexico	Common
Diamesa chiobates	Minnesota, Wisconsin	Osage Co.
Telopelopia okoboji	Iowa, Minnesota, New Mexico	Common
Lenziella cruscula	South Dakota	Common

Tanypus nubifer Coquillett, *Tanypus concavus* Roback, *Paramerina smithea* (Sublette), *Telopelopia okoboji* (Walley) and *Lenziella cruscula* Saether have been collected throughout various summer months. *T. nubifer* and *P. smithae* are more common in aquatic habitats in the high plains than elsewhere within the state. Their distribution outside the state of Kansas suggests that they may more appropriately be considered as part of a distinctive high plains fauna rather than central plains; however, additional distributional and abundance data will be needed to distinguish between these two characterizations.

T. concavus has been collected with some regularity from ponds, reservoirs and slow-moving streams in the Osage Cuestas ecophysiographic region of Kansas. Roback (personal communication) has indicated that this species is not common in any of the habitats from which it has been collected in the eastern United States.

The remaining two species, *T. okoboji* and *L. cruscula,* are common in streams and larger rivers with sand and sand/silt substrates throughout the state. They commonly are collected along with species of *"Harnischia* Com-

plex" genera such as *Robackia, Chernovskiia, Cryptochironomus* and *Cyphomella*. Sublette (personal communication) has indicated that *T. okoboji* is a dominant Pentaneurini component of sandy bottomed streams in New Mexico. The predominance of these two species in sandy bottomed streams suggests that they may have their largest populations within streams of the central plains states.

DISCUSSION

As indicated in the introduction, it was previously my feeling that the Kansas chironomid fauna would be composed of (1) cosmopolitan species, (2) species that are widespread across the eastern United States and having their westernmost distributional limits in the central plains, and (3) species that are adapted to living in shifting sand or sand/silt habitats, a common river substrate type within the central plains region. Initial investigation of the chironomid fauna of Kansas has shown this view to be an oversimplification. While it is true that many species which occur in Kansas can be readily assigned to one of the above three categories, the species discussed in this paper indicate that additional geographic distributional patterns assist in determining the faunal associations that occur within the state. From the perspective of large scale distributional patterns it would now seem that the following distributional patterns are implicated as contributing to the species richness of Kansas Chironomidae:

(1) Species with cosmopolitan distributions.
(2) Eastern species — Species widely distributed across the eastern United States whose western distributional limits are in the central plains states. In Kansas the Flint Hills generally mark the western edge of the distributional boundary.
(3) Western or southwestern species — Species recorded primarily from the west side of the Rocky Mountains, or from the southwest United States. These species appear to extend north and east into the high plains ecophysiographic region of western Kansas.
(4) Northern species — Species distributed throughout Canada and having a southern distributional extension along the Rocky Mountains and into the high plains. These species appear to be restricted in Kansas to the high plains ecophysiographic region in the western part of the state.
(5) Southeastern species — Species with dense populations in the southeast United States, but with marginal populations extending north and west into or throughout much of the central plains region.
(6) Central plains species — Species that are specifically adapted to microhabitat conditions such as shifting sand or sand/silt substrates.

Because of the predominance of these habitat conditions in the central plains, these species have their principal population densities in this region. Marginal populations of such species may occur in areas other than the central plains when appropriate localized microhabitat conditions exist; however, these populations would not be considered dominant species components of major ecophysiographic regions.

In addition to the large scale distributional influences, several subordinate influences associated with specific ecophysiographic regions in Kansas may contribute to the species richness of the state. As indicated in the results, the occurrence of *Sympotthastia* sp. in Cherokee County is most certainly associated with the influence of the Ozarkian Plateau spillover into Kansas. *Stictochironomus naevus,* which has only been collected to date within the Red Hills ecophysiographic region, may be an example of another very regionalized subordinate influence. While no data exists to date, it is likely, based upon their statewide uniqueness in terms of stream types and riparian vegetation, that the Chautauqua Hills and the Cherokee Lowlands ecophysiographic regions may yield additional Chironomidae that are restricted to these areas within the state.

LITERATURE CITED

COLER, B.G. AND A. SLATER. 1982. Additions and corrections to the list of Dytiscidae of Kansas. Tech. Publ. State Biol. Surv. Kansas 12:43-48.

BECK, W.M., JR. 1977. Environmental requirements and pollution tolerance of common freshwater Chironomidae. U.S. Envir. Prot. Agen., Cincinnati, OH. EPA-600/4-77-024. 260 pp.

FEERINGTON, L.C., JR. 1981. Kansas Chironomidae, Part I. Tech Publ. State Biol. Surv. Kansas 10:45-51.

_____. 1982. Kansas Chironomidae, Part II: The Tanypodinae. Tech. Publ. State Biol. Surv. Kansas 12:49-60.

GELHAUS, J.K. 1982. New records and distributional notes for Kansas crane flies, excluding *Limonia* (Diptera: Tipulidae). Tech. Publ. State. Biol. Surv. Kansas 12:70-88.

GILBERT, C. 1979. New records of Kansas Hydrophilidae (Insecta: Coleoptera). Tech. Publ. State Biol. Surv. Kansas 8:23-30.
——————. 1980. New records of Kansas Hydrophilidae: *Epimetopus, Helochares, Hydrochus, Laccobius,* and *Tropisternus* (Insecta: Coleoptera). Tech. Publ. State Biol. Surv. Kansas 9:54-59.
HAMILTON, S.W. AND G.A. SHUSTER. 1979. Records of Trichoptera from Kansas, II: The families Glossosomatidae, Helicopsychidae, Hydropsychidae and Rhyacophilidae. Tech. Publ. State Biol. Surv. Kansas 8:15-22.
——————. 1980. Records of Trichoptera from Kansas, III: The families Limnephilidae, Phryganeidae, Polycentropodidae, and Sericostomatidae. Tech. Publ. State Biol. Surv. Kansas 9:20-29.
HANSEN, D.C. AND E.F. COOK. 1976. The Systematics and morphology of the Nearctic species of *Diamesa* Meigen, 1835 (Diptera: Chironomidae). Mem. Amer. Entomol. Soc. 30:1-203.
HUGGINS, D.G. 1978. Additional Records of Kansas Odonata. Tech. Publ. State. Biol. Surv. Kansas 6:1-35.
——————. 1981. New state and distributional records for Kansas Plecoptera. Tech. Publ. State Biol. Surv. Kansas 10:65-70.
LIECHTI, P.M. 1978. *Stenonema* mayfly records for Kansas. Tech. Publ. State Biol. Surv. Kansas 6:53-58.
——————. 1979. *Caenis* mayfly records for Kansas. Tech. Publ. State Biol. Surv. Kansas 8:12-14.
——————. 1980. *Baetis* mayfly records for Kansas. Tech. Publ. State Biol. Surv. Kansas 9:15-19.
——————. 1981. Kansas mayfly records for the genera *Potamanthus, Pentagenia, Ephemera, Ephoron,* and *Tortopus*. Tech. Publ. State Biol. Surv. Kansas 10:52-56.
——————. 1982. Five additional Ephemeroptera genera from Kansas. Tech. Publ. State Biol. Surv. Kansas 12:13-16.
—————— AND D.G. HUGGINS. 1977. Records of Megaloptera in Kansas. Tech. Publ. State Biol. Surv. Kansas 4:45-50.
MALLOCH, J.R. 1915. The Chironomidae, or midges of Ill. with particular reference to the species occurring in the Illinois River. Bull. Ill. State Lab. Nat. Hist. 10:275-543.
MAY, E.M. 1982a. Records of *Limonia* crane flies in Kansas (Diptera: Tipulidae). Tech. Publ. State Biol. Surv. Kansas 12:89-93.
——————. 1982b. New records of Kansas *Hydrophilidae* (Insecta: Coleoptera). Tech. Publ. State Biol. Surv. Kansas 12:94-104.
OLIVER, D.R. 1981. Chironomidae, pp. 423-458 *in* McAlpine, J.F., et al., coordinators. Manual of Nearctic Diptera. Agr. Can. Monogr. 27. 674 pp.
PARKIN, R.B. AND J.B. STAHL. 1981. Chironomidae (Diptera) of Baldwin Lake, Illinois, a cooling reservoir. Hydrobiologia 79:119-128.
ROBACK, S.S. 1971. The Subfamily Tanypodinae in North America. Monogr. Acad. Nat. Sci. Phila. 17:1-410.
——————. 1981. The Immature Chironomids of the Eastern United States. V. Pentaneurini-*Thienemannimyia* group. Proc. Acad. Nat. Sci. Phila. 133:73-128.
SAETHER, O.A. 1971. Four new and unusual Chironomidae (Diptera). Can. Entomol. 103:1799-1827.
SHUSTER, G.A. AND S.W. HAMILTON. 1978. Records of the Trichopteran families Hydroptilidae, Philopotamidae and Psychomyiidae from Kansas. Tech. Publ. State Biol. Surv. Kansas 6:36-47.

SIMPSON, K.W. AND R.W. BODE. 1980. Common larvae of Chironomidae (Diptera) from New York State streams and rivers with particular reference to the fauna of artificial substrates. N.Y. St. Mus. Bull. 439. 105 pp.

SLATER, A. 1979. Additions to and corrections to the list of aquatic and semiaquatic Heteroptera of Kansas. Tech. Publ. State Biol. Surv. Kansas 8:31-37.

_____. 1980. New Records of Dryopidae and Elmidae from Kansas. Tech. Publ. State Biol. Surv. Kansas 9:60-66.

_____. 1981. Aquatic and semiaquatic Heteroptera in the collection of the State Biological Survey of Kansas. Tech. Publ. State Biol. Surv. Kansas 10:71-88.

_____. 1982. Aquatic and semiaquatic Heteroptera in the collection of the State Biological Survey of Kansas: Addendum. Tech. Publ. State Biol. Surv. Kansas 12:39-42.

STEWART, K.W. AND D.G. HUGGINS. 1977. Kansas Plecoptera (Stoneflies). Tech. Publ. State Biol. Surv. Kansas 4:31-40.

SUBLETTE, J.E. 1960. Chironomid midges of California. I Chironominae, exclusive of Tanytarsini (=Calopsectrini). Proc. U.S. Nat. Mus. 112:197-226.

TOWNES, H.K., JR. 1945. The Nearctic species of Tendipedini (Diptera: Tendipedidae (=Chironomidae)). Amer. Midl. Natur. 34(1):1-206.

The Distribution of Chironomids in Geothermal Waters in New Zealand

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ABSTRACT. — The fauna of geothermal waters of North Island, New Zealand, has a low number of species most of which are insects. Chironomid larvae usually dominate these communities and are pre-adapted to geothermal waters with temperatures up to 36°C and acidity as low as pH 1.8. All species belonged to the Tanypodinae and Chironominae. There were no obligate acidophiles and only one possible thermophile. Often only one chironomid species was found at each site suggesting that each species occupies a narrow niche.

Geothermal waters generally support a limited biota which, because of its low species diversity and the small variations in flow, temperature and chemical composition of these waters, may be considered simpler to study than most other ecosystems. General investigations of the fauna of geothermal waters are few, mostly confined to Algeria (Mason, 1939); Iceland (Tuxen, 1944); USA (Brues, 1927, 1932); New Zealand (Winterbourn, 1968, 1969, 1970, 1973; Winterbourn and Brown, 1967; McColl and Forsyth, 1973; Forsyth & McColl, 1974; Forsyth, 1977; Forsyth and MacKenzie, 1981).

The fauna is mainly confined to insects, which are possibly favoured because of the protection from the harsh conditions afforded by their chitinous exoskeleton, and most are forms which breathe atmospheric oxygen. Exceptions within the latter group are the chironomid larvae which often dominate the fauna and which, in the absence of fish, may be at the top of the food chain directly above the primary producers.

The temperature boundary separating a diverse fauna at ambient temperatures from a restricted fauna at warm temperatures in New Zealand is between 25° and 30°C. The upper temperature limits for most thermally adapted invertebrates fall between 32°C and 45°C. Chironomid larvae, especially the Chironominae, can tolerate extremes of environmental conditions and some are pre-adapted to warm or cold acid waters or warm neutral waters of the Taupo volcanic zone of North Island, New Zealand, where they may reach unusually high population densities in the absence of competition and their normal predators.

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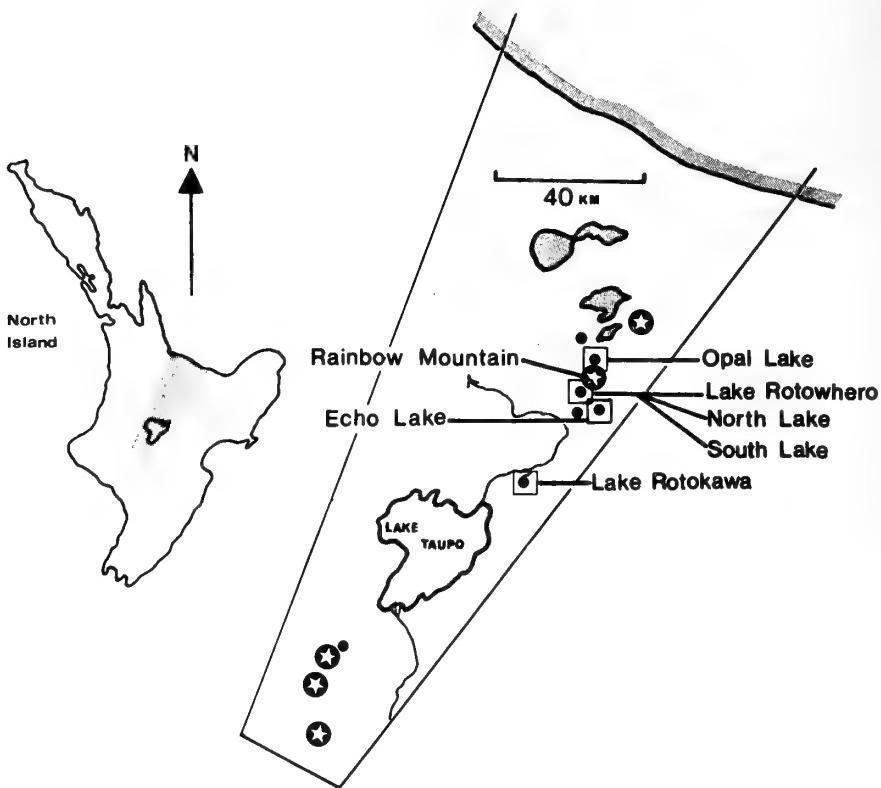
FIG. 1.   Taupo volcanic zone of North Island, New Zealand, showing sites of standing geothermal waters (●) and volcanic cones (✪).

In this paper the species distribution of chironomid larvae is examined in relation to pH and temperature and the abundance of algae, expressed as chlorophyll *a*, in the water.

The Taupo volcanic zone (Fig. 1) is part of a belt of volcanism extending from the central volcanic plateau of North Island, New Zealand, to the Kermadec Trench. In this zone are a variety of lakes, springs, streams and seepages under various degrees of geothermal influence. Ten sites were sampled at least once in winter, when water temperatures of neighbouring cold, monomictic lakes were between 8° and 10°C. These sites fell more or less into two groups depending on their pH. Standing waters usually were more acid than flowing waters. If hot springs enter a lake after only limited exposure to the atmosphere, the H_2S is oxidised to H_2SO_4, and the pH is

lowered. However, if the spring water is more fully exposed to the air as in flowing waters, the H_2S is rapidly lost to the atmosphere and the pH is little changed.

RESULTS

Standing waters (Fig. 1, Table 1)

1. Lake Rotowhero: This lake is both acid and thermal. It has an area of 2.5 ha and a maximum depth of 14 m, pH 3.1, and a minimum water temperature of 29.5°C. Geothermal water enters the lake through several springs at the lake margin. The mean concentration of chlorophyll *a* was 48.0 mg.m^{-3}. The algae comprised two species of *Chlorella*. The fauna was limited to insects (apart from a rare copepod) with larvae of *Chironomus zealandicus* dominant at a maximum concentration of 31 000 m^2 in winter. The larvae disappeared in spring when the water temperature exceeded 34°C to reappear in autumn when the temperature fell below 34°C. The chironomid larvae were eaten by a Notonectid, *Anisops wakefieldi* and a damsel-fly *Ischnura aurora*. Considerable adult mortality was inflicted by insectivorous birds. Other insects present were a thermal mosquito *Culex rotoruae,* a Hydrophilid and two Dytiscid beetles and two Hemipterans.

2. Lake Rotokawa: This lake has an area of 62 ha and a mean depth of 5 m. There is a small geothermal input, but it is a cold lake with winter temperatures similar to those of other cold lakes in the area. There are only larvae of *Chironomus zealandicus* in Lake Rotokawa and these are confined to depths up to 1 m. The chlorophyll *a* concentration in the lake in mid summer was 115.0 mg.m^{-3} derived from a large population of *Euglena* and less abundant *Chlamydomonas*. The only other benthic invertebrate was a leech, *Helobdella* sp.

3. Echo Lake has an area of about 3 ha and is 34 m deep. The water was turbid with sulphur particles and the concentration of algal pigment was at the limits of detection. On the other hand there was a large concentration of bacteria. The concentration of dissolved oxygen was never more than 0.5 g.m.$^{-3}$ and pH was 2.4. The water temperature through the water column was a uniform 19.5°C. No benthic invertebrates were present, but abundant larvae of the mosquito *Culex rotoruae* were near the lake margin. This species is confined to thermal waters of the Taupo volcanic zone.

4. Opal Lake: This has an area of 0.5 ha and a maximum depth of 5 m. There was a large population of flagellate algae and the concentration of chlorophyll *a* was 42 mg.m^{-3}. The waters were cold and the pH was 4.3. There was no obvious inflow or outlet. The acid character of the water was probably due to H_2S from a nearby fumarole. The chironomid fauna was

TABLE 1.   Distribution of chironomid larvae and other insects of relation to pH, temperature °C, and concentration of chlorophyll a (mg.m^{-3}) in thermal waters of the Taupo volcanic zone of North Island, New Zealand. (− = no record).

	pH	t°C	Chlorophyll a	Macropelopia umbrosa	Chironomus zealandicus	Kiefferulus opalensis	Paratanytarsus agameta	Tanytarsus funebris	Tanytarsus sp.	Culex rotoruae	Liodessus plicatus	Enochrus tritus	Ephydridae	Microvelia macgregori
Standing waters														
Lake Rotowhero	3.1	29.5	48		+					+	+	+	+	+
Lake Rotokawa	2.1	10.0	115		+							+	+	+
Echo Lake	2.4	19.5	0.2							+				+
Opal Lake	4.3	8.5	42	+	+	+	+				+			+
North Lake	1.8	14.0	0.4		+						+			
South Lake	2.5	8.5	0.8		+			+						
Flowing waters														
Ketetahi Springs	6.0	32.0	—		+		+						+	
Waiotapu Springs	6.4	17.0	0.2		+				+	+			+	+
Waimangu Stream	4.2	36.0	1.7		+				+	+		+	+	
Crater Outlet	5.5	36.0	1.5											

more diverse here than in the other locations examined (Table 1) perhaps because of a less extreme geothermal influence. Opal Lake is the type locali- . ty for *Kiefferulus opalensis* the larvae of which were abundant in crevices of the bark of submerged branches at the lake edge. Unlike the other species present *Kiefferulus* was rare in the sediments. *Chironomus zealandicus* was always dominant at a mean concentration of 4470 larvae.m^{-2}. Larvae of *Macropelopia umbrosa* were 1150 m^{-2}, but were not recorded from elsewhere in the region. The parthenogenetic *Paratanytarsus agameta* appeared only in autumn. Other insects belonged to Odonata, Trichoptera, Hemiptera and Ceratopogonidae. Oligochaetes were found in this lake but not in the others mentioned in this paper.

5. Rainbow Mountain Lakes: Rainbow Mountain crater contains two small lakes of about 0.2 ha each. North Lake is 8 m deep with a pH of 1.8 and a water temperature of 14°C in winter. Hot water enters as condensate from a fumarole 2 m from the lake edge. The concentration of chlorophyll *a* was 0.4 mg.m^{-3}. Clumps of senescent filamentous alga *Cladophora* sp. were at the surface and on the lake bed. A few larvae of *Chironomus zealandicus* were observed amongst the floating algae but there were none in the sediment. The water was turbid with sulphur particles and other mineral material. This is the lowest pH at which chironomids have been recorded in New Zealand.

South Lake about 8 m away, is 3 m deep with a pH of 2.5. The water is greenish and more optically clear than that of North Lake. The chlorophyll *a* concentration of the water was 0.8 mg.m^{-3} and the water temperature was 8.5°C indicating no input of hot water. Larvae of *Chironomus zealandicus* were abundant in the sediment, while floating mats of filamentous alga *Microspora pachyderma* supported numerous larvae of *Tanytarsus funebris*. Adults of both species were emerging abundantly in winter when the water temperature was 8.5°C. Elsewhere chironomid emergence was not obvious at this temperature.

Flowing waters (Fig. 2, Table 1)

1. Ketetahi Springs: Ketetahi Springs on the slopes of Mt Tongariro at an altitude of 1385 m above sea level is an area of numerous hot springs and fumaroles of different physical and chemical characteristics. Most of the springs were near boiling, turbid, and coloured by metal sulphides, but some were clear. Algal mats of *Phormidium* sp. and a coccoid blue-green alga *Synechoccus* sp. grew on the margins of one stream at a temperature of 53°C and pH 6.0. Downstream the spring became a thin film of water crossing a terrace of deposited iron hydroxide (limonite). Here larvae of *Paratanytarsus agamenta* built their tubes at a density of about 20 000.m^{-2}. In the mud and silt of small, shallow pools along its course were a few lar-
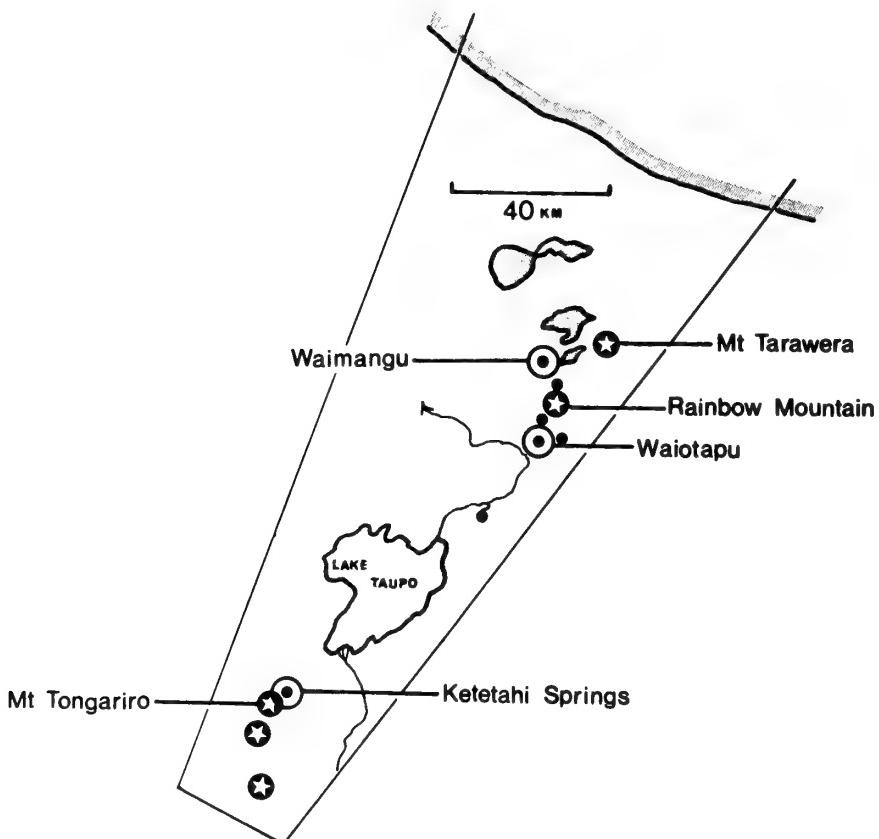
FIG. 2. Taupo volcanic zone of North Island, New Zealand, showing sites of flowing geothermal waters (●) and volcanic cones (✪).

vae of *Chironomus zealandicus*. The upper temperature limit of both species was 32°C.

2. Waiotapu: At Waiotapu thermal area the Champagne Pool overflows at 73°C on to the Artist's Palette, a flat area of siliceous sinter overlain by fine silt and mud. Here the water temperature was 18°C and the pH 6.4. Abundant larvae of *Chironomus zealandicus* were exposed when the mud was disturbed. No other invertebrates were present.

3. Waimangu Valley: Waimangu Valley is a thermal area formed during the eruption of nearby Mt Tarawera in 1886. Frying Pan Lake, pH 3.8 and water temperature 56°C drains into the Waimangu Stream. Numerous hot springs along the stream margins supported large populations of larvae of

TABLE 2. Lower limits of pH and upper limits of water temperature for chironomids in thermal waters of the Taupo volcanic zone, North Island, New Zealand.

	pH	t °C
Macropelopia umbrosa	4.3	25.0
Chironomus zealandicus	1.8	34.0
Kiefferulus opalensis	4.3	25.0
Paratanytarsus agamenta	4.3	32.0
Tanytarsus funebris	2.5	25.0
Tanytarsus sp.	4.2	36.0

Tanytarsus sp. which built their tubes in shallow pools at water temperatures up to 36°C and at pH 4.2. Adults were emerging from the slow flowing pools and swarming at the stream margin during the winter inspection. Larvae of *Culex rotoruae* were found with them. Despite an extensive search, only one larva of *Chironomus zealandicus* was found here. Filamentous algae *Phormidium* sp. and *Mastigocladus* sp. with unicellular blue-green *Synechoccus* sp. were common particularly at higher temperatures. The same biota was present in a small stream draining the Inferno Crater at Waimangu where the pH was 5.5 (Table 1). Concentrations of chlorophyll *a* in both streams were less than 2 mg.m^{-3}.

DISCUSSION

All chironomids found in New Zealand geothermal waters belong to the Chironominae and Tanypodinae in contrast to some northern hemisphere hot springs where Orthocladinae have also been reported.

Although six species of chironomid were found in geothermal waters, only Opal Lake (4 species), Ketetahi Springs, South Lake on Rainbow Mountain and Waimangu Stream (2 species) had more than one species. The greater diversity in Opal Lake was probably due to the higher pH, low water temperature and relatively high concentration of chlorophyll *a*. Nevertheless *Macropelopia umbrosa* and *Keifferulus opalensis,* although widespread, have a local distribution. In South Lake and Ketetahi Springs the species exploit different niches.

Paratanytarsus agameta at Ketetahi Springs was probably living close to its upper temperature limit. It is not characteristic of thermal areas, but common in small, shallow, sheltered ponds where the summer water temperatures may briefly approach the winter temperatures measured at Ketetahi Springs. However, it may be unable to tolerate summer temperatures there. *Tanytarsus funebris* is recorded for the first time from

acid waters. Its usual habitat is in ponds, sewage waters and the littoral zone of lakes. The presence of *Chironomus zealandicus* at most of these sites illustrates its adaptability to extreme conditions. *C. zealandicus* and *Tanytarsus* sp. are the only species that appear to be truly heat tolerant, and *C. zealandicus* and *Tanytarsus funebris* are the only species tolerant of extreme acid conditions. The mildly acid tolerant species, *Kiefferulus opalensis* and *Macropelopia umbrosa* have been found in neutral waters.

Tanytarsus sp. may be the only obligate thermophile for it has not been found outside the Waimangu thermal valley. No chironomids are obligate acidophiles (Table 2). Likewise none of the other common invertebrates are obligate acidophiles, but *Culex rotoruae* and the Ephydrid flies are confined to thermal water. The Ephydrid flies were at all sites where there was hot flowing water. *Microvelia macgregori* was found only in standing waters (Table 1). It was rare for geothermal waters at temperatures below 36°C not to support chironomids. An exception was Echo Lake where chlorophyll *a* was virtually absent. At the other sites where the concentration of chlorophyll *a* was low, water was flowing exposing the larvae to more food.

Algae appear to be essential for the support of chironomids in geothermal waters. Chironomid larvae are a characteristic element in this environment which supports a restricted insect community. A notable feature of these geothermal waters is that despite the spatial differences of temperature, water flow, and food availability at any one site, often only one species of chironomid is found there. Each species, therefore, appears to occupy a narrow niche in these extreme conditions.

REFERENCES

BRUES, C.T. 1927. Animal life in hot springs. Quarterly Review of Biology 2:181-203.
—————. 1932. Further studies on the fauna of North American hot springs. Proceedings of the American Academy of Arts and Sciences 67:185-303.
FORSYTH, D.J. 1977. Limnology of Lake Rotokawa and its outlet stream. New Zealand Journal of Marine and Freshwater Research 11:525-539.
FORSYTH, D.J. AND R.H.S. McCOLL. 1974. The limnology of a thermal lake: Lake Rotowhero, New Zealand. II. General biology with emphasis on the benthic fauna of chironomids. Hydrobiologia 44:91-104.
FORSYTH, D.J. AND A.L. MACKENZIE. 1981. Limnology of Opal Lake. New Zealand Journal of Marine and Freshwater Research 15:279-283.

McColl, R.H.S. and D.J. Forsyth. 1973. The limnology of a thermal lake: Lake Roto-whero, New Zealand. I. General description and water chemistry. Hydrobiologia 43: 313-332.

Mason, I.L. 1939. Studies on the fauna of an Algerian hot spring. Journal of Experimental Biology 16:487-498.

Tuxen, S.L. 1944. The Hot Springs of Iceland. Einer Munksgaardd, Copenhagen. 216 p.

Winterbourn, M.J. 1968. The faunas of thermal waters of New Zealand. Tuatara 16: 111-122.

_____. 1969. The distribution of algae and insects in hot spring thermal gradients at Waimangu, New Zealand. New Zealand Journal of Marine and Freshwater Research 3:459-465.

_____. 1970. The Hydrophilidae (Coleoptera) of New Zealand's thermal waters. Transactions of the Royal Society of N.Z., Biological Science 12:21-28.

_____. 1973. Ecology of the Copland River warm springs, South Island, New Zealand. Proceedings of the N.Z. Ecological Society 20:72-78.

Winterbourn, M.J. and T.M. Brown. 1967. Observations on the faunas of two warm streams in the Taupo thermal region. New Zealand Journal of Marine and Freshwater Research 1:38-50.

Effect of Metabolites on the Pyruvate Kinase of Chironomus plumosus Larvae

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ABSTRACT. — Pyruvate kinase from *Chironomus plumosus* larvae was tested for regulatory characteristics of the last one-directional step in glycolysis. Due to the addition of KHCO₃ to the assay, the pH rose and the enzyme activity decreased. From the metabolites tested only the addition of ATP results in a decrease of activity. Alteration of the pH shows the greatest influence on the activity of the PK.

The pyruvate kinase (PK) catalyses the last one-directional step in the anaerobic degradation of glycogen. Therefore, it was assumed to be a control enzyme of glycolysis (Newsholm & Start 1977).

During anaerobic metabolism in chironomid larvae, this reaction leads to the formation of lactate, ethanol and alanine (Frank 1977, 1983). The influence of ATP, fructose-1, 6-biphosphate, $KHCO_3$ and of endproducts on the PK from 4th instar larvae of *Chironomus plumosus* should be shown.

MATERIAL AND METHODS

For all experiments, dredged 4th instar larvae of *Chironomus plumosus* and *Glyptotendipes paripes* from Tegeler Lake and Lake Heiligensee were used. The larvae were kept in plastic jars with tap water and no food the last two days before use.

Enzyme assay. — The homogenisation medium contained 0,5 ml/25 mg wet weight of larvae, 20 mM Tris-HCl buffer, pH 7,2,1 mM MgCl. The clear supernatant (10″ × 1000 g) was used for the assay at 25°C, 334 nm. The reaction was started by adding the supernatant fraction. Maximum reaction velocities were obtained under the following conditions, 1 ml volume: ATP: pyruvate-phosphotransferase E.C. 2.7.1.40 after Hoffman *et al.* (1979): 50 mM Tris-HCl buffer pH 7,2; 1 mM ADP; 0,1 mM fructose-1,6-biphosphate; 10 mM $MgSO_4$; 75 mM KCl; 0,14 mM NADH; 12,0 mM phosphoenolpyruvate; 7 U/ml LDH; 50 ul supernatant.

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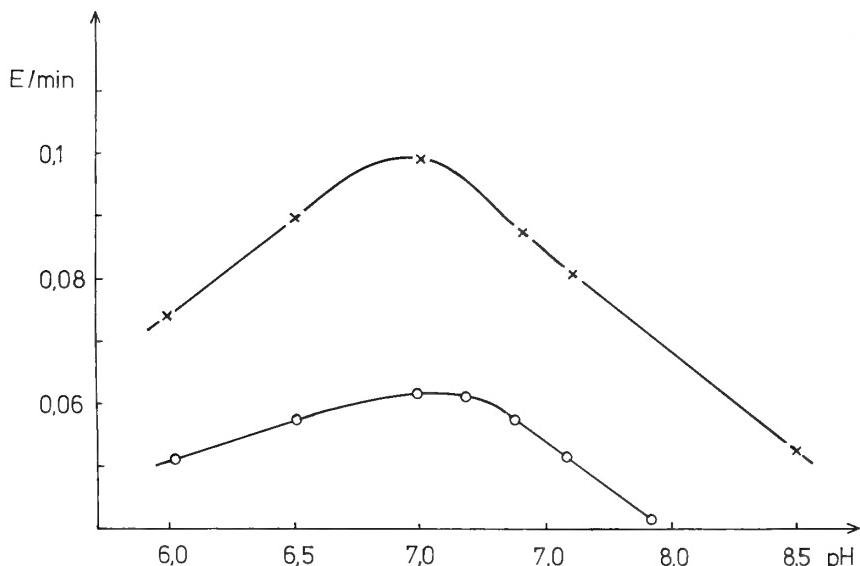
FIG. 1.   pH dependencies of pyruvate kinase activity, $\triangle E/min$, o Tris buffer, x Tea buffer.

RESULTS AND DISCUSSION

The pH-dependency of the enzyme activity shows a maximum between pH 6,8-7,2. Different buffers show the same course but varying activities (Figure 1). KHCO₃ was added to the test mixture to simulate the carbon dioxide formed during anoxia. The addition of 250 mM $KHCO_3$ results in a decrease of activity by 50%, both in *Chironomus plumosus* and *Glyptotendipes paripes* larvae. Measurements of the pH of the assay mixture showed a rise in the pH. The decrease of activity is more a result of the alteration of the pH than of the addition of $KHCO_3$ (Figure 2).

The addition of 5 mM (Tris buffer) or 10 mM ATP (TEA buffer) results in a decrease of activity by 82-92%. The addition of 1 mM fructose-1,6-biphosphate results in a reactivation of the PK (Fig. 3).

The addition of endproducts of the anaerobic metabolism to the assay mixture (up to 5 mM) showed no significant differences to the control values. Only the influence of 5 mM alanine results in a light increase in activity.
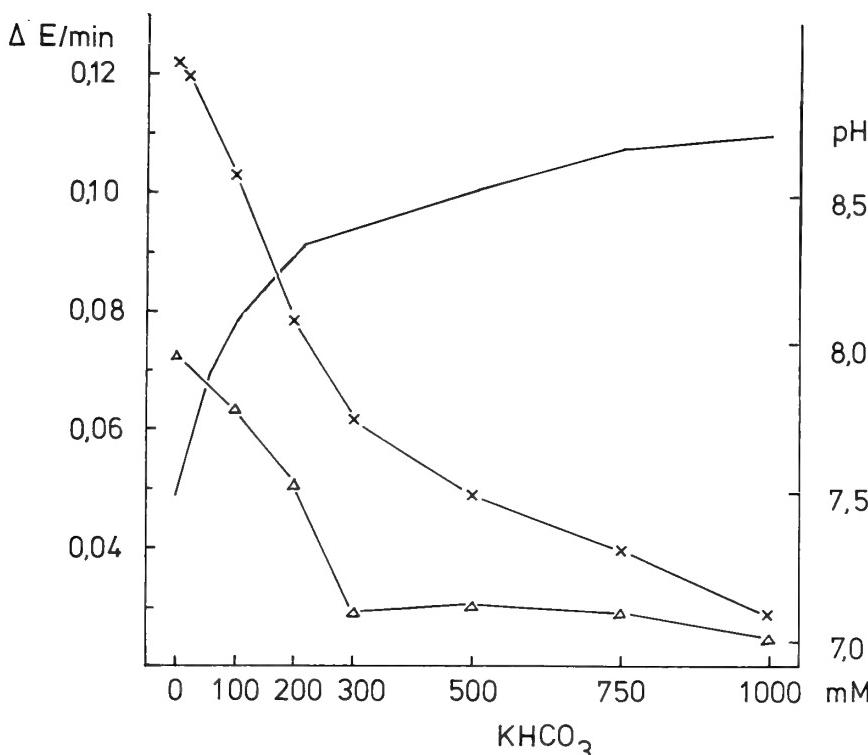
FIG. 2. Effect of KHCO₃ on the activity of pyruvate kinase from *Chironomus plumosus* (△) and *Glyptotendipes paripes* (×) larvae. — pH alteration by addition of KHCO₃ to the assay.

The maximum metabolic concentration of endproducts of *Chironomus plumosus* larvae measured during anoxia are:

0,12 mM/g wet weight lactate
0,3 mM/g wet weight ethanol
0.01 mM/g wet weight alanine

Only unphysiologically high concentrations of metabolites (≥5 mM) show an influence on the activity of the PK, but they show no regulatory effect.

The greatest influence on the activity of the PK results from the alteration of the pH as also shown by Hoffman *et al.* (1979). Holwerda *et al.* (1981) pointed out that in Mytilus, PK is the regulate in the last step of anaerobic glycolysis. In this species, the addition of 1 mM alanine to the assay results in a inhibition of activity by more than 75%. The activity of PK from
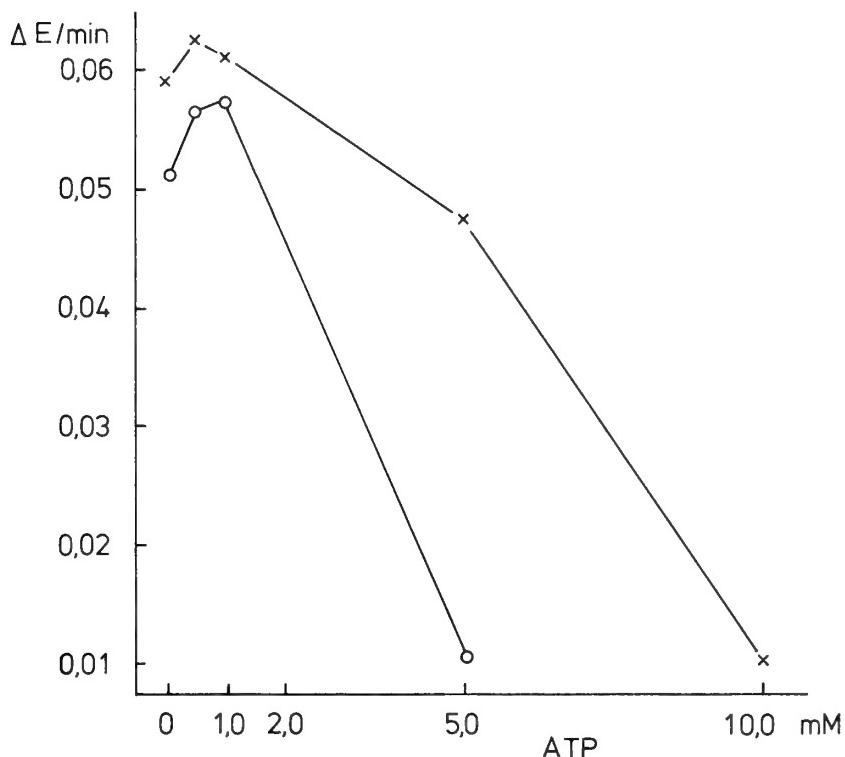
FIG. 3.   Effect of ATP on the activity of pyruvate kinase from *Chironomus plumosus* larvae, o Tris buffer, x Tea buffer.

Chironomus during anaerobiosis will increasingly be inhibited through the effects of alteration of pH and not by alanine.

The activation of *Chironomus* PK by fructose-1,6-biphosphate shows patterns similar to those described by Munday *et al.* (1980). The activation of the PK could be interpreted as a feed-forward mechanism at the beginning of the anaerobic metabolism to ensure that the activity of PK is increased in relation to the activity of phosphofructokinase.

In *Chironomus* the PK shows no allosteric characteristics. The regulation of the glycolysis in *Chironomus* might occur at the phosphofructokinase step as pointed out by Castellini and Somero (1981).

REFERENCES

CASTELLINI, M.A. AND G.N. SOMERO. 1981. Buffering capacity of vertebrate muscle: Correlations with potentials for anaerobic funktion. — J. comp. Physiol. 143, 191-198.

FRANK, C. 1977. Ökologie und anaerober Stoffwechsel der Larven von *Chironomus plumosus* L. (Diptera, Nematocera). Diss. Universität Tübingen.

————. 1983. Ecology, production an anaerobic metabolism of *Chironomus plumosus* L. larvae in a shallow lake. II Anaerobic metabolism. — Arch. Hydrobiol. [96:354-363].

HOFFMANN, K.H., T. MUSTAFA AND J.B. JORGENSEN. 1979. Role of pyruvate kinase, phosphoenolpyruvate carboxykinase, malic enzyme and lactate dehydrogenase in anaerobic energy metabolism of *Tubifex* sp. — J. comp. Physiol. 130, 337-345.

HOLWERDA, D.A., P.R. VEENHOF AND H.A.A. VAN HEUGTEN. 1981. Regulation of mussel pyruvate kinase during anaerobiosis. — Posterabstract, 3d Congr. Europ. Soc. Comp. Physiol. Biochem. Noordwijkerhout.

MUNDAY, K.A., G.I. GILES AND P.C. POAT. 1980. Review of the comparative biochemistry of pyruvate kinase. — Comp. Biochem. Physiol. 67 B, 403-411.

NEWSHOLME, E. A. AND C. START. 1977. Regulation des Stoffwechsels, Verlag Chemie, Weinheim. 305 pp.

Ecology and Importance of the Chironomidae in the Trophic Structure and Biocenosis of Zoobenthos in the Lakes of the National Park of the Lithuanian SSR

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ABSTRACT. — Twenty-five lakes in the National Park of the Lithuanian SSR were studied from 1976 to 1980 to determine the distribution of chironomid larvae according to sediment type, depth, and other environmental factors. Eighteen of these lakes are ranked according to an index of density and an index of biomass. The problem of sediment composition, as a significant factor in the distribution and development of chironomid larvae, was examined.

INTRODUCTION

Twenty-five lakes (Fig. 1) in the National Park of the Lithuanian SSR were investigated from 1976 to 1980. These lakes are located in the hills of eastern Lithuania (Grigelis et al., 1982) and differ in various topographical conditions. The total area of these lakes was 3680.7 ha. Some lakes, such as Gavys, Gavaitis, Vajuonis, Kretuonas, Usiai and others are artificially excluded from the territory of the National Park as these lakes are more intensively used for recreational purposes. The lakes differ in surface area, depth, form of bed, length of orientation of their principal axis, width, and in their relationship to the direction of the prevailing westerly winds (Grigelis et al., 1975).

RESULTS

The investigation of the benthic fauna of 25 lakes in the National Park of the Lithuanian SSR from 1976 to 1980 showed that in the sublittoral and profundal zones of some lakes the dominant group of zoobenthos in terms of species composition, distribution, density and biomass was the Chironomidae. *Chironomus plumosus, C. anthracinus, Sergentia longiventris,* and *Procladius* spp. were widely distributed in these fresh water basins.

On the basis of an index of density and biomass (Fig. 2, 3), the chironomids in the investigated lakes could be subdivided into four groups:

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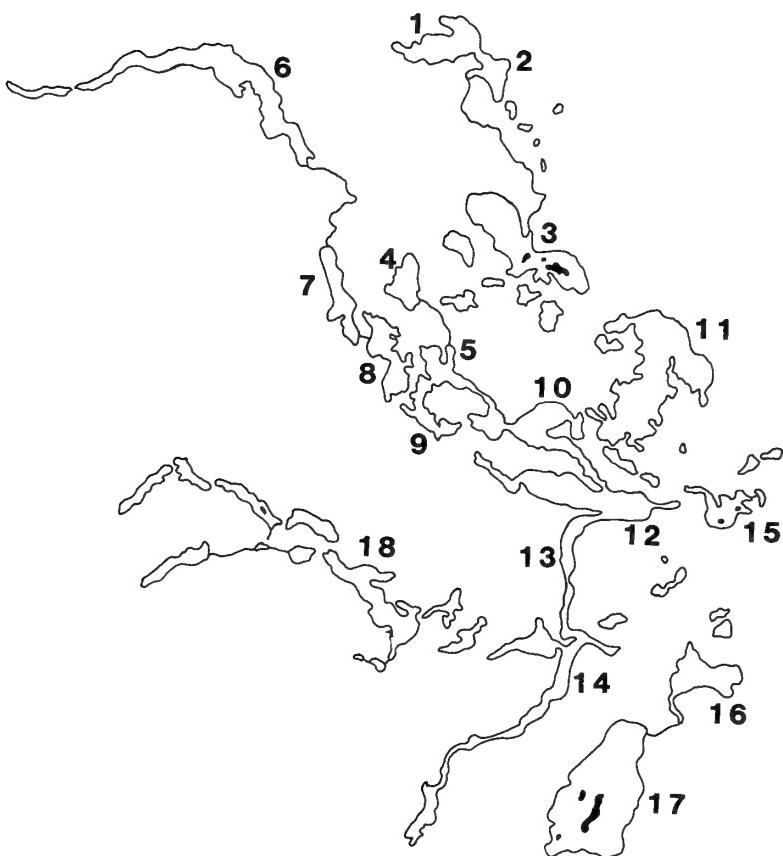
FIG. 1.   Map of the larger lakes of the National Park of the Lithuanian SSR: 1. Utenas, 2. Utenykstis, 3. Baluosas, 4. Almajas, 5. Asekas, 6. Tauragnas, 7. Pakasas, 8. Ukojas, 9. Linkmenas, 10. Asalnai, 11. Dringis, 12. Lušiai, 13. Šakarvai, 14. Žeimenys, 15. Gavys, 16. Vajuonis, 17. Kretuonas, 18. Usiai.

1). Lakes in which the Chironomidae were the most important group constituting from 50.0 to 83.3 percent of the abundance and from 56.8 to 94.3 percent of the biomass. The lakes of this group differed in depth and substrate. Lakes Lušiai, Asalnai, and Tauragnas are deep with *Sergentia longiventris* as the dominant chironomid. Lakes Gruodiškis, Taramas, and Dringykštis are shallow with *Chironomus plumosus* as the dominant chironomid.
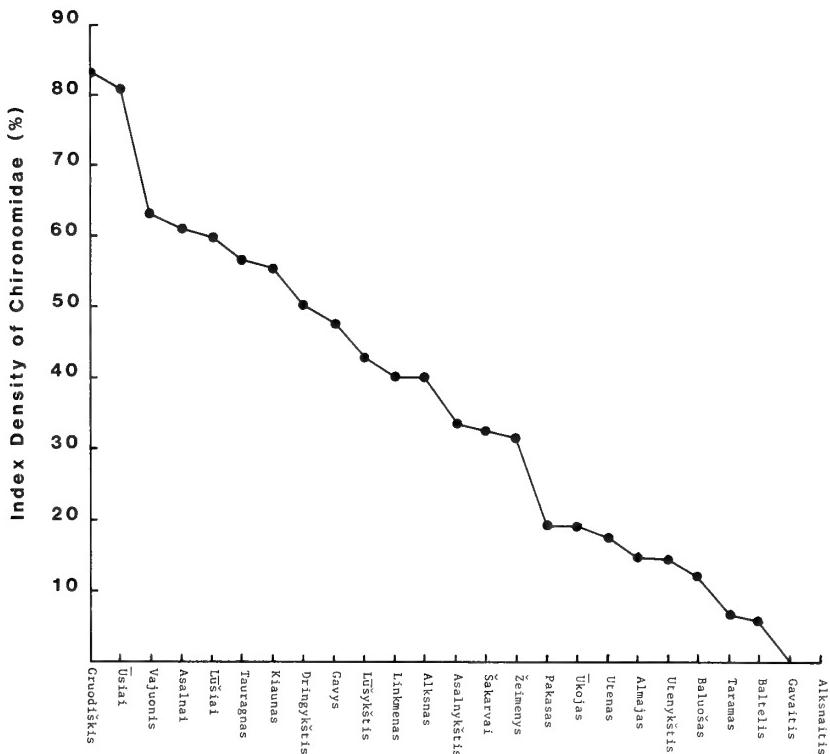
FIG. 2.   Distribution of the lakes of the National Park of the Lithuanian SSR according to the index of density for chironomids.

2). Lakes in which the Chironomidae were the second most important group of organisms constituting from 31.5 to 50.0 percent of the abundance and from 23.7 to 45.7 percent of the biomass. These lakes are both deep and shallow lakes as in group 1.

3). Lakes in which the Chironomidae were the second or third most important group of organisms constituting from 12.0 to 19.0 percent of the abundance and from 14.3 to 21.4 percent of the biomass.

4). Lakes in which the Chironomidae were the third most important group of organisms or were absent, constituting from 0.0 to 6.8 percent of the abundance and from 0.0 to 10.0 percent of the biomass. These are lakes with hydrotroilite.

The distribution, species composition, and development of the Chironomidae depends upon such factors as water temperature, chemical and physical properties (Grigelis et al., 1981; Žukaite, 1980), sediments,
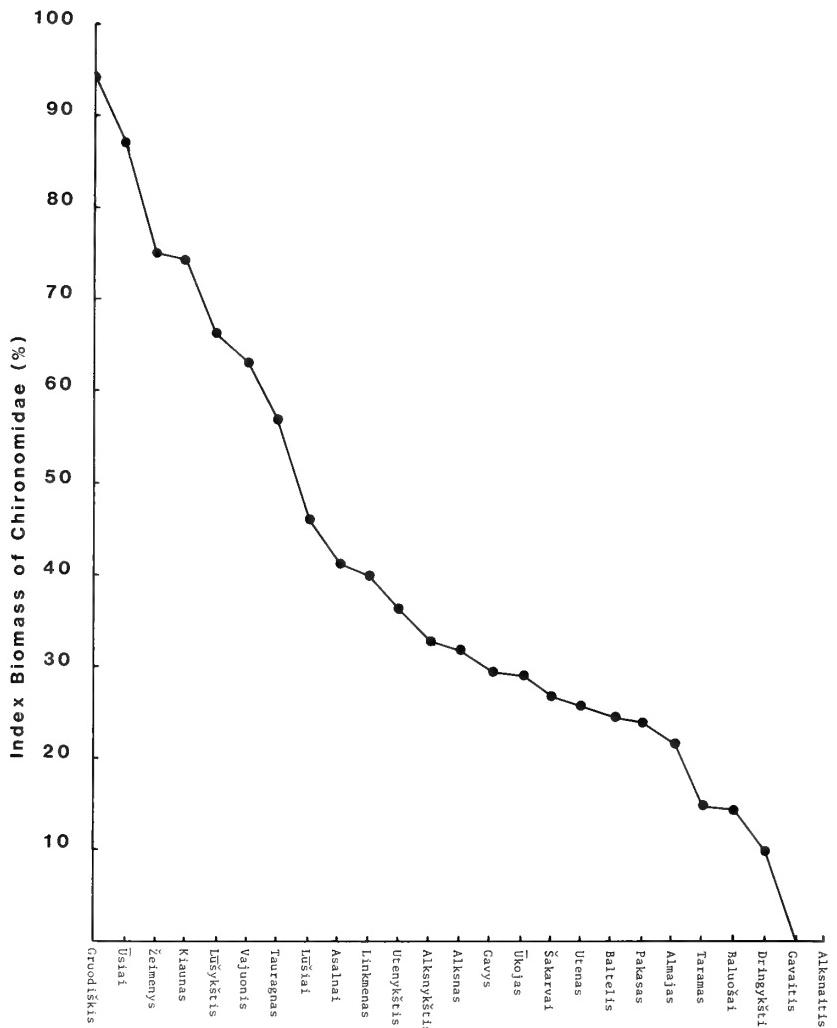
FIG. 3.   Distribution of the lakes of the National Park of the Lithuanian SSR according to the index of biomass for chironomids.

microflora of the substrate, vegetation cover, and other environmental factors.

In the profundal zone of the deep lakes the cold stenotherm larvae of *Sergentia longiventris* were the dominant organism in Lakes Šakarvai, Lušiai, Gavys, and Tauragnas, with *Chironomus anthracinus* the dominant organism in the profundal zone of Lake Dringis. The thickness of the

hypolimnion in these lakes varied from 50 to 20 m and occupied a dominant position in the total volume of the lake.

Lakes Taramas, Baltelis and Utenykstis, which had hydrotroilite in the bottom were poor in chironomids. Lakes Alksnaitis and Gavaitis had hydrotroilite in the bottom and had no chironomids. These latter two lakes were chaoborid lakes.

Our data confirms the distribution dependence of chironomid larvae on water temperature in the hypolimnion and bottom sediments.

LITERATURE CITED

GRIGELIS, A., G. BALKUVIENE, J. BANIONIENE, B. GAIVENIS, O. NAINAITE, AND E. ŽUKAITE. 1975. Hydrobiological reserches in the Lithuanian lakes. In Lithuanian with English and Russian summaries.

GRIGELIS, A., G. BALKUVIENE, J. BANIONIENE, E. ŽUKAITE, J. KAVALIAUSKIENE, R. LENKAITIS, O. NAINAITE, A. ORLOVA, AND V. SUKACKAS. 1982. Biological productivity of lakes of the National Park of the Lithuanian SSR. I. Hydrobiological characteristics. Lietuvos TSR Mokslu Akademijos darbai, C serija 3(79):54-63. In Russian with Lithuanian summary.

GRIGELIS, A., R. LENKAITIS, O. NAINAITE, AND E. ŽUKAITE. 1981. Peculiarities of distribution of cold-stenotherm hydrobionts in lakes of the National Park of the Lithuanian SSR. Verh. Internat. Verein. Limnol. 21:501-503.

ŽUKAITE, E. 1980. Thermal regime of Lušiai and Šakarvai lakes during period of summer thermal stagnation in 1978. Lietuvos TSR Mokslu Akademijos darbai, B serija 6(121): 83-91. In Russian with Lithuanian summary.

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Appearance and Behavior of Nigerian and Californian Chironomid Larvae during Recovery from Desiccation

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ABSTRACT. — Samples of dry substrate material containing Nigerian *Polypedilum* sp. near *vanderplanki* Hinton and Californian *Tribelos atrum* (Townes), *Phaenopsectra pilicellata* Grodhaus, and *Hydrobaenus* sp. were examined after immersion in water. Samples contained instars II, II-III, or II-IV, depending on the species. Each species demonstrated a characteristic folding or curling of the dormant larvae, which, except for *Polypedilum,* were enclosed in cocoons. After wetting, recovery took place most rapidly in *Polypedilum* and most slowly in *Phaenopsectra.* In *Polypedilum* it took 11-120 min for the first muscle contractions and 45-135 min for a return to normal appearance. In *Phaenopsectra* it took 11 hr-5 days for the first muscle contractions and 12-48 hr for a return to near normal appearance. *Polypedilum* is suited to life in rock hollows, in which both inundation and drying are apt to occur suddenly. The Californian species are adapted to the vernal pool environment, in which hydrodynamic processes proceed at a slower rate; their life histories are probably regulated by diapause.

Certain aquatic chironomid larvae are able to suspend activity for long periods of time while their habitat is without water. Chironomidae with this adaptation have been reported from Africa (Hinton 1951, Miller 1969, McLachlan and Cantrell, 1980), Australia (Edward 1968, Jones 1974), and North America (Grodhaus 1976, Grodhaus and Rotramel 1980, Wiggins et al. 1980). The present paper compares species from Nigeria and California with regard to the gross changes that occur while they recover from desiccation. The Nigerian species that we studied appears to be related to both *Polypedilum vanderplanki* Hinton and *P. dewulfi* Goetghebuer but resembles *P. vanderplanki* more closely, on the basis of the single female

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reared from our sample. As were the larvae of *P. vanderplanki* studied by Hinton (1951, 1960, 1968), our African specimens were obtained from rock cavities. Our Californian larvae have been identified as *Tribelos atrum* (Townes), *Phaenopsectra pilicellata* Grodhaus, and an undescribed species of *Hydrobaenus,* each of which inhabits vernal pools (Grodhaus 1980). Owing to the lack of specimens at the proper stage of recovery, the drought-resistant *Polypedilum* reported by Grodhaus and Rotramel (1980) was not included in the study.

MATERIALS AND METHODS

African material was collected from "grinding" hollows on "inselberg" rocks near Zaria, northern Nigeria on 30 March 1973 by L. Knutson. Hollows as small as 10 cm long, 5 cm wide, and 5 cm deep yielded viable larvae. The larvae from California were extracted from soil from vernal pool sites listed by Grodhaus (1980).

Dry substrate materials (i.e. debris from grinding hollows or soil from vernal pool sites) were stored in polyethylene bags prior to examination. All samples were wetted before examination to minimize mechanical damage to the larvae. *Polypedilum* larvae were abundant in the sample and were relatively easy to find. The other species required concentration by sieving and washing (Grodhaus 1980). Specimens were placed in dishes of tap water and observed at 10-60x. Additionally, specimens in cocoons had to be released mechanically with forceps to be seen.

Specimens were stored and examined at room temperature (ca 21°C) unless noted otherwise. Results pertaining to different instars of a given species were pooled. Observations of material stored for similar lengths of time but from different localities were also combined.

RESULTS

Dormant larvae remain essentially unchanged for a few minutes after being wet. When in that condition, specimens were considered to be in their "drought phase", which was used as a reference point for describing changes occurring later, during which time specimens were referred to as being in their "recovery phase".

Drought Phase Larva: All recently wetted larvae appeared completely lifeless. No cast skins or fecal pellets were associated with them to indicate activity during storage. Water content of the specimens has not been determined, but soil samples matched with samples yielding viable *Tribelos* after 23 months of storage contained 4-5% water.

Drought phase larvae of each species showed visible evidence of desiccation. The antennae, anterior prolegs, anal papillae, and preanal setae were appressed against the body, and the oral cavity often contained an air vacuole. In *Polypedilum* and *Tribelos,* the body segments were shrunken, i.e. compressed, contracted, or both. The condition of *Phaenopsectra* was drastically different; the larva was inflated to near normal proportions, but a large vacuole occupied almost all of the interior of each body segment. This vacuolization caused larvae to float. *Hydrobaenus* larvae have not been studied critically enough to describe their condition in detail.

The color of the recently wetted larvae was brownish red to yellowish red in *Polypedilum* and *Phaenopsectra,* yellowish red in *Tribelos,* and faint yellow in *Hydrobaenus.*

Table 1 shows which instars were represented in the dry substrates. Viability was demonstrated by each stage except *Polypedilum* instar II, which was scarce in the sample. Proportions of instars were rather constant in samples from California, with instar II predominating in all instances.

Table 1 also indicates the type of covering associated with the drought phase larva. Definite cocoons are constructed by *T. atrum, P. pilicellata,* and *Hydrobaenus* sp. (See Grodhaus 1980 for descriptions.) Some larvae of *Polypedilum* sp. were seen to be within a cell lined with a silken membrane (Fig. 1). The membrane surrounding the illustrated specimen appears to be open at the anterior end. Whether all *Polypedilum* larvae were similarly encased was not ascertained. The membrane of *Polypedilum* was far less durable than that forming the wall of the Californian type cocoon, which could survive rough treatment and could be recognized long after the larva had emerged from it.

All larvae whose recovery was observed were initially in a species-specific resting position (Table 1). The three species that assumed body folds were assigned positional indices according to the system of Danks (1979). The larva of *Hydrobaenus* sp. was not folded at any point but was curled inside its cocoon in a position similar to that figured for *Eukiefferiella claripennis* (Lundbeck) by Madder et al. (1977).

Recovery Phase Larva.   Table 2 shows the interval between the exposure of specimens to water and the first muscular movements observed in three species. Prolonged storage seemed to retard the recovery of *Tribelos* and *Phaenopsectra.* The kinds of contractions and their usual sequences were: *Polypedilum*—rhythmic pulsation of pharynx; rhythmic pulsation of dorsal vessel; contraction of body, head, and mandibles; crawling. *Tribelos*—contraction of prolegs and body; irregular contraction of dorsal vessel; contraction of head and mandibles; crawling. *Phaenopsectra*—occasional contraction of body and head and irregular contractions of dorsal vessel; gradually

TABLE 1.   Condition of desiccated larval Chironomidae.

Species	Instar	Resting position*	Description of surrounding material
Polypedilum sp (nr. vanderplanki)	II III IV	6.5.1	Delicate silk membrane, probably doesn't enclose larva completely
Tribelos atrum	II III	11.1	Cocoon, encloses larva completely
Phaenopsectra pilicellata	II III	4.4.4	Cocoon, encloses larva completely
Hydrobaenus sp.	II	curled	Cocoon, encloses larva completely

*According to Danks (1971), i.e., numerals indicate numbers of body segments and periods indicate where folds occur.

TABLE 2.   Recovery of desiccated larval Chironomidae.

Species	No. of specimens	Period of dry storage (months)	Estimated time elapsed from immersion to:	
			1st muscle contraction	cessation of water uptake
Polypedilum sp. (nr. vanderplanki)	7	54-56	11-120 min	45-135 min
Tribelos atrum	1	1	30 min	50 min
"	4	9-17	10-150 min	10-150 min
"	7	23-30	235-240 min	300 min
"	4	84*	16 hr	200 min
Phaenopsectra pilicellata	9	5-12	11-34 hr	12-30 hr
"	2	18	20-40 hr	20 hr
"	3	30-36	20 hr-5 days	20 hr
"	2	60	30-40 hr	40-48 hr

*Kept at ca 4°C; others kept at room temperature.

stronger, more complex movements leading to crawling (after termination of diapause, as discussed below). Viable *Hydrobaenus* sp. larvae were making simple contractions after several days, similarly to *Phaenopsectra*.

The contractions of the pharynx and dorsal vessel that occurred in nearly all of our *Polypedilum* larvae were similar to the movements of *P.*

vanderplanki observed by Hinton (1951, 1960). These contractions appeared before any other movements in *Polypedilum*. In *Tribelos* and *Phaenopsectra,* pulsations of the dorsal vessel seemed to occur only after major body movements had begun, and these genera did not exhibit pharyngeal pulsations.

After being wet for 48 hours, most larvae had made movements in one of the above categories or were clearly dead. An exceptional specimen of *Phaenopsectra,* however, did not show even simple contractions until it had been wet for 5 days. Most of the other *Phaenopsectra* specimens listed in Table 2 continued making only simple contractions for many days. This semiactive condition is presumed to be associated with diapause in which full mobility is delayed until after the larvae have been chilled for several weeks (Grodhaus 1980). *Polypedilum* and *Tribelos* larvae regularly began to crawl within the first 20 hours.

During the early stages of recovery, specimens take up water until they either regain their normal appearance or reach a certain stable appearance. It is assumed that rehydration is complete in the first case and nearly complete in the second. The point where one or the other form of stability is reached is referred to in Table 2 as the time of "cessation of water uptake". In *Polypedilum* and *Tribelos,* rehydration is complete within a short period, but in *Phaenopsectra* the larva slowly enters a stage where it is still somewhat flaccid, though all of its vacuoles have been replaced by haemolymph. Full rehydration in *Phaenopsectra* probably takes place when diapause is completed and the larva regains full mobility.

DISCUSSION

Cocoon construction is associated with numerous species of chironomids that are aquatic during their entire larval life (Danks 1971). For these species, the cocoon-making behavior is an adaptation to cold winter conditions. As pointed out by Wiggins et al. (1980), a change in timing is all that would be needed to convert the behavior pattern of cold-tolerant species to one suited to temporary habitats. The timing of the building of cocoons by certain drought-resistant species is probably regulated by their state of development (Grodhaus 1980), not by receding water.

The habit of larvae going into folded or curled positions in the substrate might be thought of as protection against too rapid movement of water through the tissues. Our results, however, indicate that water uptake is faster in the twice-folded *Polypedilum* than it is in the once-folded *Tribelos,* so it appears that the rate is not governed by the amount of folding. *Polypedilum* sp. near *vanderplanki* is anomalous in that its larva engages in
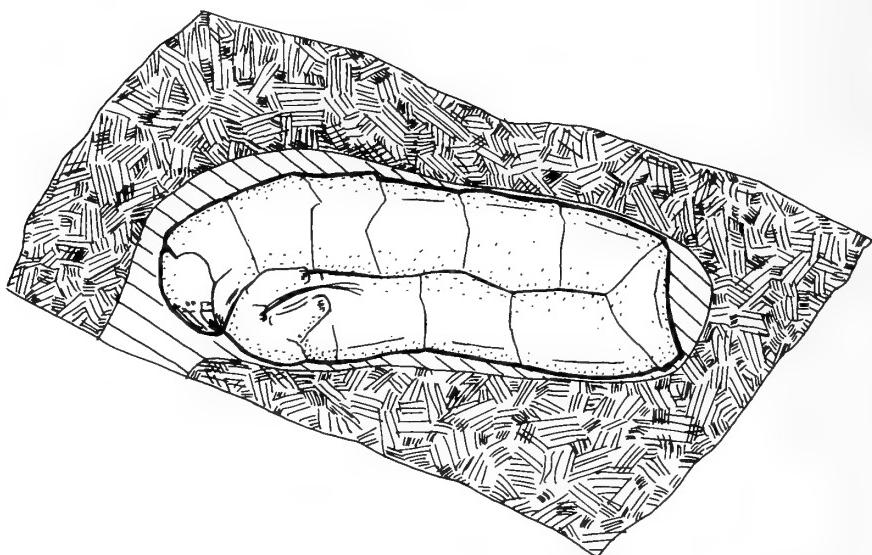
FIG. 1.   Instar III *Polypedilum* sp. near *vanderplanki* in a piece of substrate material approximately 15 min. after wetting.

folding without making a cocoon. Danks and Jones (1978) have suggested that a drawing of Hinton's (Fig. 7, 1968) shows a cocoon of *P. vanderplanki*. This illustration could also be interpreted as a folded larva without a definite cocoon, comparable to the specimen, in Fig. 1 of the present paper. It is indeed possible that neither folding nor cocoon formation is obligatory. With regard to several Californian species, however, the present study and a previous one (Grodhaus 1980) indicate that viable larvae are invariably folded and encased in cocoons.

It is tempting to think that a cocoon might reduce the amount of water lost by a larva during drought, but we do not believe this to be the case. Becoming dehydrated to an extreme degree may actually be advantageous. It has been suggested that dehydration permits *P. vanderplanki* to withstand higher temperatures than would otherwise be possible (Hinton 1960). Our visual observations, indicating severe dehydration in both Nigerian and Californian species, should be substantiated by moisture content measurements. A study by Jones (1975) indicates than another chironomid, *Paraborniella tonnoiri* Freeman, is only slightly dehydrated in its dormant state, during which this species can withstand drying of its rock-hollow habitat in Australia.

The protective value of the cocoon may simply be concealment for the Californian vernal pool chironomids. Larvae probably build their cocoons well in advance of the drying of the pools. In an exposed state they would become increasingly subject to attack as predaceous insects invade the pools.

The habitat of the *Polypedilum* species of the present study is similar to that described by Hinton (1950) for *P. vanderplanki*. Hinton noted that northern Nigerian rock cavities contain water intermittently during March and April and consistently from May until December. Especially during the first rains, these cavities are capable of rapid filling and drying. Larvae inhabiting such an environment would have to be quick to respond to hydrodynamic changes and would probably not be benefitted by having a diapause. As would be expected, *Polypedilum* is quick to regain mobility and to become fully hydrated in response to wetting alone.

The Californian species inhabit large depressions on the ground, which require considerable precipitation before surface water appears. In a typical year, the earth becomes damp in October or November, after which an aquatic environment exists from December until March or April. Both the filling and drying processes take place slowly. Revival of the Californian species is slow, and the presence of water may only start the recovery process. The life histories of these species are probably regulated by diapause, in which larvae do not complete their metamorphosis until after they have been exposed to low temperatures (Grodhaus 1980), a pattern that fits the climate in northern California, in which cool weather and rain coincide.

REFERENCES

DANKS, H.V. 1971. Overwintering of some north temperate and arctic Chironomidae. II. Chironomid biology. Can. Entomol. 103:1875-1910.

DANKS, H.V., AND J.W. JONES. 1978. Further observations on winter cocoons in Chironomidae (Diptera). Can. Entomol. 110:667-669.

EDWARD, D.H. 1968. Chironomidae in temporary freshwaters. Aust. Soc. Limnol. Newsl. 6:3-5.

GRODHAUS, G. 1976. Two species of *Phaenopsectra* with drought-resistant larvae (Diptera: Chironomidae). J. Kans. Entomol. Soc. 49:405-418.

_____. 1980. Aestivating chironomid larvae associated with vernal pools. P. 315-322 *in*: Chironomidae. Ecology, systematics, cytology and physiology. (D.A. Murray, editor). Pergamon Press, Oxford.

GRODHAUS, G., AND G.L. ROTRAMEL. 1980. Immature stages of *Polypedilum pedatum ex-celsius* (Diptera, Chironomidae) from seasonally flooded tree-holes. Acta Univ. Carol. Biol. 1978:69-76.

HINTON, H.E. 1951. A new chironomid from Africa, the larva of which can be dehydrated without injury. Proc. Zool. Soc. Lond. 121:371-380.

_____. 1960. Cryptobiosis in the larvae of *Polypedilum vanderplanki* Hint. (Chiro-nomidae). J. Ins. Physiol. 5:286-300.

_____. 1968. Reversible suspension of metabolism and the origin of life. Proc. R. Soc. B171:43-57.

JONES, R.E. 1974. The effects of size-selective predation and environmental variation on the distribution and abundance of a chironomid, *Paraborniella tonnoiri* Freeman. Aust. J. Zool. 22:71-89.

_____. 1975. Dehydration in an Australian rockpool chironomid larva *(Para-borniella tonnoiri)*. Proc. R. Entomol. Soc. Lond. A49:111-119.

MADDER, M.C., D.M. ROSENBERG, AND A.P. WIENS. 1977. Larval cocoons in *Eukief-feriella claripennis* (Diptera: Chironomidae). Can. Entomol. 109:891-892.

MCLACHLAN, A.J., AND M.A. CANTRELL. 1980. Survival strategies in tropical rain pools. Oecologia 47:344-351.

MILLER, P.L. 1970. On the occurrence and some characteristics of *Cyrtopus fastuosus* Bigot (Dipt., Stratiomyidae) and *Polypedilum* sp. (Dipt., Chironomidae) from temporary habitats in western Nigeria. Entomol. Mon. Mag. 105:233-238.

WIGGINS, G.B., R.J. MACKAY, AND I.M. SMITH. 1980. Evolutionary and ecological stra-tegies of animals in annual temporary pools. Arch. Hydrobiol. Suppl. 58:97-206.

Lotic Chironomids of the North Carolina Mountains

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ABSTRACT. — Five years of chironomid data from streams and rivers in the North Carolina mountains have been combined to generate both a taxa list and some seasonal information. Approximately 172 species were recorded. The seasonal patterns observed for the more abundant taxa were often consistent with limitation by temperature and/or photoperiod, with 8 winter taxa, 21 summer taxa and 12 spring-fall taxa. However, 16 taxa had multiple peaks spread throughout the year. Temporal separation of some species may explain niche division within a diverse chironomid community; examples are given for 2 genera. The total chironomid community also showed seasonal variation with peaks in December-January, May-June and September. It is important to consider this normal seasonal variation when using indicator species concepts.

Introduction

The benthic macroinvertebrate community is frequently used as an indicator of water quality. Chironomidae comprise a large proportion of this community, but they are often treated as a single taxon in many routine surveys. This loss of information originates from both taxonomic uncertainties and difficulty in evaluating chironomid data. The latter problem can be addressed through the compilation of good "baseline" information. This investigation utilizes existing information collected by the North Carolina Division of Environmental Management to compile a list of larval Chironomidae collected from streams and rivers in the mountain regions of North Carolina.

Data Sources

Quantitative information comes from 934 "kick" samples (Frost *et al.* 1971) collected from 1978 to 1982. This particular collection technique can be utilized in a wide variety of lotic habitats and gives very consistent results (Pollard and Kinney 1979). Qualitative information is available from about 50 other sites. Chironomidae collected by Gurtz (1982) from streams in the Cowetta National Forest have also been utilized in this survey.

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The quantitative information (kick samples) has been sorted by month to compile frequency (F) data. Monthly frequencies have been calculated as number of collections of a taxon divided by the total number of collections in any given month. The total number of collections in each month varied from 26 (November) to 170 (August). Average monthly abundance/sample ($\bar{N}$) was also calcuated for the most abundant taxa. Both F & $\bar{N}$ can be used to generate the expected seasonal distribution of mountain chironomids.

Results and Discussion

Table 1 lists larval chironomid taxa collected from North Carolina mountain streams and rivers. This list includes at least 172 species. Where several species (or species groups) are known to exist, but have not been routinely separated, the estimated number is given in parentheses.

Many of the genera in Table 1 could not be easily dealt with at the species level. In particular, the *Cricotopus/Orthocladius* (C/O) group presents a special problem. We initially listed taxa in this group as C/O sp. 1, C/O sp. 2, etc. This "in-house" number has been retained in Table 1 to maintain consistency with prior publications. There are many species in the C/O group. Single samples often have 4-6 C/O group species. Coffman (1973) listed 23 *Cricotopus/Orthocladius* species for a Pennsylvania stream. We have recorded at least 26 species in the North Carolina mountains. Pollution tolerance also varies widely within the C/O group, therefore, accurate identification is needed to use this group in environmental assessment.

Table 2 lists the estimated chironomid taxa richness, by group, for our mountain samples. An estimate is also given for all DEM sampling, including Piedmont and Coastal Plain areas. The estimate for the entire mountain area (168 species) is not much greater than species richness recorded by Coffman (1973) for a single 3rd order stream (143 species). If the species richness values are converted to a percentage within each subfamily, the results are remarkably similar to other investigations of lotic Chironomidae. Lindegaard-Peterson (1972) and Boerger (1981) cite many studies with results comparable to North Carolina data.

Seasonal trends for stream chironomids have usually been addressed through studies of adult emergence. Emergence patterns have been related to changes in temperature and photoperiod (Aagaard 1978). The seasonal patterns observed in Table 1 are also consistent with regulation by temperature and/or photoperiod.

Several different types of seasonal patterns are illustrated in Figs. 1-4. Approximately 8 low temperature, (winter) species were found; examples are shown in Fig. 1. *Orthocladius* (*Euorthocladius*) sp. 3 is a eurythemal (broad temperature range) species with 3 maxima October to April, but it is

largely absent in July and August. *Diplocladius cultriger* is an example of a stenothermal (narrow temperature range) winter species, having a single maximum in November-December. This is in rough agreement with emergence data given by Coffman (1973) for this species, showing a single emergence period in February-April. Approximately 21 warm temperature (summer) species were found; examples are presented in Fig. 2. *Cricoptopus bicinctus* is a eurythermal species with maxima occurring from April to October. *Polypedilum illinoense* and *Robackia demeijerei* have a more restricted seasonal distributions, with a pronounced maximum in July. Approximately 12 species had spring-fall maxima; examples are given in Fig. 3. Another common pattern is seen in species having three or more maxima (approximately 16 taxa, see Fig. 4). This pattern may reflect either multiple generations or the combination of several species which are taxonomically inseparable. The seasonal curve shown for *Diamesa* could represent 1 summer species and 1 spring-fall species. Likewise, the seasonal curve for *Micropsectra* could be attributed to a combination of a winter species, a spring-fall species and a summer species.

The distinct seasonality of most chironomid species suggest that "indicator species" concepts must take into account normal seasonal variation. For example, some of the *Cricotopus* species which are associated with toxic conditions (C. *infuscatus* gr.) will normally be absent, or present in very low numbers, during winter months.

The various seasonal patterns may be related to the concept of "niche division." The chironomid community of a stream usually comprises a very large proportion (up to 50%) of the benthic macroinvertebrate species (Coffman 1973). How do so many species coexist without competitive exclusion? Investigators studying the zooplankton and phytoplankton communities in freshwater lakes have addressed a similar question. Hutchinson (1961) posed the "Paradox of the plankton," contrasting the apparently uniform nature of the plankton environment with a highly diverse planktonic community. Subsequent studies have shown many different ways in which zooplankton species divide up the planktonic habitat. For example, Makarewicz and Likens (1975) showed that the major zooplankton taxa in Mirror Lake could be differentiated in relation to seasonality, depth preference and food size.

Information is accumulating to suggest that chironomid species avoid competitive exclusion by similar mechanisms (Ramcharan & Patterson 1978). Several studies have shown spatial separation of chironomid species by means of substrate preferences (Jankovic 1979, Lindegaard-Petersen 1972). Chironomids also may show different preferences along the stream contanuum. Penrose *et al.* (1982) have demonstrated that certain

TABLE 1. Chironomid Taxa from North Carolina Mountain Streams & Rivers.

Taxon	Frequency (# collections)	Total # Collected		Data by Month 1	2	3	4	5	6	7	8	9	10	11	12	Other Data
TANYPODINAE (16)																
Ablabesmyia ornata	3	3	F(%)	—	—	—	—	—	—	—	2	—	—	—	—	
A. mallochi	3	3	F(%)	—	—	—	—	—	1	—	—	2	—	—	—	
A. parajanta	—	—														X
A. tarella	—	—														X
Brundiniella sp.	—	—														X
Conchapelopia gr. (4+)	270	1527	F(%)	35	23	15	24	36	44	37	28	32	22	31	22	
			N̄	1.1	1.4	0.3	1.0	2.3	1.5	2.1	1.7	0.7	1.6	6.7	3.8	
Labrundinia neopilosella	—	—														X
L. nr. pilosella	—	—														X
Natarsia sp.	—	—														X
Nilotanypus sp.	—	—														X
Procladius bellus	—	—														X
P. subletti	2	2	F(%)	—	—	—	—	—	—	—	—	2	—	—	—	
Zavrelimyia spp.	1	1	F(%)	—	—	—	—	—	1	—	—	—	—	—	—	
CHIRONOMINI (38)																
Chironomus spp.	22	65	F(%)	3	1	1	2	2	2	3	5	—	2	15	—	
Cladopelma sp.	—	—														X
Cryptochironomus blarina	1	1	F(%)	—	—	—	—	—	—	—	1	—	—	—	—	
C. fulvus gr.	36	78	F(%)	8	2	3	4	—	6	—	7	4	2	—	—	
Cryptotendipes sp.	3	4	F(%)	1	—	—	—	—	—	—	—	2	1	—	—	
Demicryptochironomus sp.	34	53	F(%)	—	—	3	6	—	11	7	6	2	—	—	—	

Taxon	n	N	type													X
Dicrotendipes spp.	3	3	F(%)	—	—	—	—	—	—	—	—	2̲	—	1	—	
D. nervosus	—	—														X
D. neomodestus	—	—														X
Endochironomus nigricans	2	9	F(%)	—	—	—	—	—	2	—	2	—	—	—	—	X
Genus nr. Beckiella	1	1	F(%)	—	—	—	—	—	2	—	—	—	—	—	—	X
Glyptotendipes sp.	1	1	F(%)	—	—	—	—	—	—	—	—	—	—	—	—	
Kiefferulus dux			F(%)	—	—	4	—	9	12̲	7	11̲	8	6	27̲	19	X
Microtendipes spp. nr. pedellus	114	936	N̄	25̲	13	17	—	—	—	—	—	—	—	—	—	
	8	29	F(%)	6.4	.13	0.8	0.1	0.5	0.1	0.5	0.1	0.1	0.5	1.4	0.4	
M. nr. ryadalensis			F(%)	—	—	—	—	—	3	10̲	—	1	1	—	—	
Parachironomus monochromus	4	7	F(%)	2	—	—	—	—	—	—	2	—	—	—	—	X
Paracladopelma undine	—	—														
P. sp. 1 (Jackson)																X
Paralauterborniella nigrohalterale	—	—														
Paratendipes spp.	6	20	F(%)	1	—	1	—	2	2	3	—	—	—	—	—	
Phaenopsectra spp. (2)	—	—														X
P. flavipes	—	—													12̲	X
Polypedium angulum	44	99	F(%)	1	—	9	5	6	4	3	5	9̲	—	—		
P. avicep/convictum (2)	315	3024	N̄	0.9	—	—	3.5	14.9	6.1	3.8	6.3	4.4	1.9	0.8	0.1	
P. fallax	44	103	F(%)	2	2	—	9	11̲	3	3	5	10̲	5	—	2	
P. halterale	21	49	F(%)	3	—	—	—	8	6̲	—	4	2	—	—	—	
P. illinoense	52	132	F(%)	1	—	1	5	6	5	23̲	14	9	3	—	—	
P. laetum	1	1	F(%)	—	—	—	1	1	—	—	—	—	—	—	—	
P. scalaenum	20	56	F(%)	1	2	—	2	5	6̲	3	4	1	—	—	—	
P. tuberculum	1	1	F(%)	—	—	—	—	—	1	—	—	—	—	—	—	
Pseudochironomus sp.	1	1	F(%)	1	—	—	—	—	—	—	—	—	—	—	—	

TABLE 1 (Con't)

Taxon	Frequency (# collections)	Total # Collected		Data by Month												Other Data
				1	2	3	4	5	6	7	8	9	10	11	12	
Robackia claviger	—	—														X
R. demeijerei	34	59	F(%)	—	—	—	5	11	3	20	8	2	—	—	2	
Saetheria tylus	12	41	F(%)	—	—	1	5	—	1	—	1	4	—	—	—	
Stenochironomous spp.	10	11	F(%)	1	—	1	—	3	1	3	3	—	—	—	—	
Stictochironomous sp.	12	152	F(%)	8	—	—	—	—	—	—	1	2	1	3	—	
Tribelos spp.	38	147	F(%)	6	—	4	—	—	6	—	8	10	—	—	—	
TANYTARSINI (18)																
Cladotanytarsus spp.	26	91	F(%)	—	2	2	5	5	6	3	5	—	2	—	—	
C. sp. 2	—	—														
C. sp. 5	—	—														
Constempellina sp.	1	4	F(%)	—	—	1	—	—	—	—	—	—	—	—	—	
Micropsectra spp. (4+)	116	1082	F(%)	27	2	21	9	1	17	7	2	22	1	4	33	
			Ñ	6.0	—	1.5	0.6	0.1	1.9	0.3	—	0.9	—	0.4	0.9	
Paratanytarsus spp.	3	7	F(%)	—	—	—	—	—	2	—	1	—	—	—	2	
Rheotanytarsus spp. (2+)	331	7122	F(%)	30	25	18	25	20	36	67	37	64	48	15	38	
			Ñ	40.8	5.9	2.4	1.5	0.4	4.9	11.3	9.1	31.0	23.7	0.5	5.3	
Tanytarsus spp. (3+)	98	355	F(%)	4	10	13	9	15	16	20	13	12	4	—	7	
			Ñ	0.1	0.2	0.5	0.2	0.8	0.8	0.6	0.5	0.4	0.1	—	0.2	
T. (Sublettea) coffmani	28	46	F(%)	—	—	1	2	5	6	—	7	8	—	—	—	

Taxon	N	Stat	1	2	3	4	5	6	7	8	9	X
Stempellina cf. montivago	10	F(%)	—	—	—	—	—	—	—	—	4	X
Stempellinella spp.	15	F(%)	2	—	—	—	—	—	—	—	—	
DIAMESINAE (9)												
Diamesa spp. (3+)	231	F(%)	10	25	41	32	10	23	22	35	33	
	2277	N̄	0.3	1.2	4.6	3.9	0.1	1.2	0.9	9.0	2.4	
Odontomesa fulva	—	F(%)	—	—	2	2	3	36	7	—	2	X
Pagastia spp.	99	F(%)	20	21	2	3	13	12	7	—	—	
	611	N̄	2.8	0.8	0.1	0.1	0.1	1.6	0.5	0.6	—	
Potthastia gaedi	49	F(%)	—	—	6	5	3	3	9	21	5	
P. longimanus	65	F(%)	8	8	14	3	7	4	10	4	9	
—Prodiamesa olivacea	3	F(%)	2	—	—	1	—	—	13	—	—	
Sympotthastia zavreli	—	F(%)	—	—	—	—	—	—	—	—	—	X
ORTHOCLADIINAE (91)												
Brillia spp.	139	F(%)	23	12	10	7	18	19	13	23	21	
	787	N̄	0.5	0.5	0.3	0.2	0.6	0.7	0.2	2.2	1.0	
B. parva (rare)	—											
B. modesta (rare)	—											
B. flavifrons	—											
Bryophaenocladius sp.	1	F(%)	—	—	—	1	1	—	—	—	7	
	1	N̄	2	15	—	9	2	—	—	32		
Cardiocladius spp.	171	F(%)	—	15	—	—	13	30	15	32	23	
	1176	N̄	0.1	0.3	0.2	0.2	0.2	3.0	0.8	3.2	2.2	
Chaetocladius sp.	3	F(%)	1	—	—	—	—	—	—	—	—	
Corynoneura spp. (2+)	6	F(%)	2	—	1	1	3	5	—	—	3	
Cricotopus/Orthocladius (=C/O)	91	F(%)	—	—	—	—	3	5	8	13	—	
C/O sp. 55												
Cricotopus (Nostococladius) sp.	1	F(%)	1	—	—	—	—	—	—	—	—	

TABLE 1 (con't)

Taxon	Frequency (# collections)	Total # Collected		1	2	3	4	5	6	7	8	9	10	11	12	Other Data
									Data by Month							
C/O sp. 1			F(%)	4	2	7	28	26	21	33	34	31	31	8	10	10
Cricotopus (C.) bicinctus	199	2603	N̄	—	—	0.3	2.9	3.3	3.8	1.6	3.2	2.2	9.5	—	1.0	
C/O sp. 5			F(%)	4	4	7	12	35	19	20	21	14	26	35	7	7
C. (C.) infuscatus gr.	151	2553	N̄	0.4	—	0.1	0.9	22.8	1.1	1.7	1.9	0.8	2.1	7.2	0.1	
C/O sp. 6			F(%)	—	—	4	17	8	14	17	20	24	12	4	—	—
C. (C.) varipes gr.	107	737	N̄	—	—	0.5	0.5	0.2	1.5	2.7	0.9	1.2	1.6	0.2	—	
C/O sp. 14																
C. (C.) nr. cylindraceus	7	44	F(%)	—	—	—	—	—	—	—	3	1	2	—	—	—
C/O sp. 46																
C. (C.) vieriensis gr.	10	48	F(%)	—	—	—	—	3	—	10	4	—	—	—	—	—
C.O. sp. 50																
C. (C.) trifascia	3	20	F(%)	—	—	—	—	—	3	—	—	—	—	—	—	—
C/O sp. 32																
C. (C.) sp. 1	4	5	F(%)	—	4	1	—	2	—	—	—	—	—	—	—	—
C/O sp. 9																
C. (Isocladius) nr. sylvestris	5	36	F(%)	—	—	—	—	—	4	—	—	1	—	—	—	—
C/O sp. 7																
Orthocladius (O.) dorenus gr.	70	598	F(%)	15	13	3	19	26	1	—	—	1	4	—	7	
C/O sp. 10			F(%)	24	10	18	35	18	9	3	4	3	3	19	21	
O. (O.) obumbratus gr.	128	3001	N̄	5.0	0.2	2.2	4.5	1.9	0.2	—	0.1	0.1	0.1	2.7	28.8	
C/O sp. 12																
O. (O.) cf. robacki	13	67	F(%)	1	—	6	—	2	2	—	3	2	—	—	—	—

Taxon	n	N̄		1	2	3	4	5	6	7	8	9	10	11	12	13
C/O sp. 54	48			4	6	2	2	2	12	7	—	4	3	3	12	14
O. (O.) clarkei gr.		322	F(%)	0.1	0.4	—	—	—	1.9	0.2	—	0.1	0.1	0.6	1.9	0.2
C/O sp. 47	28															X X
O. (O.) nigrius gr. (2)		152	F(%)	5	—	3	1	—	2	2	—	—	—	6	—	19
C/O sp. 33	5															
O. (O.) sp. 1		8	F(%)	—	—	—	—	—	2	2	2	—	—	—	—	—
C/O sp. 35	8															
O. (O.) sp. 2		20	F(%)	1	1	—	5	—	2	2	—	2	—	—	—	—
C/O sp. 36	6															
O. (O.) sp. 3		101	F(%)	—	—	—	—	—	6	—	—	—	2	2	—	2
C/O sp. 37	2															
O. (Euorthocladius) Type II sp.		3	F(%)	1	—	—	—	—	—	—	—	—	1	—	4	—
C/O sp. 62	4															
O. (E.) Type II sp. 2		16	F(%)	—	1	—	—	—	—	—	—	—	—	4	—	—
C/O sp. 37A	—															
O. (E.) Type II sp. 3		—														
C/O sp. 2	24															
O. (E.) sp. 1		42	F(%)	1	4	2	9	6	2	—	1	—	2	2	—	2
C/O sp. 3	31		F(%)	1	—	—	2	2	3	7	11	3	3	2	—	2
O. (E.) sp. 2		304	F(%)	25	37	30	47	38	15	3	3	9	9	24	38	43
C/O sp. 13	227		N̄	0.7	1.1	1.0	3.9	6.3	0.5	0.1	0.1	0.5	1.7	13.7	2.1	
O. (E.) sp. 3		1792	F(%)	1	—	1	16	24	15	7	12	8	2	3		9
C/O sp. 20	83		N̄	—	—	—	0.8	3.5	0.8	0.1	0.6	0.2	—	—		0.2
O. (E.) sp. 4		520														
C/O sp. 29	7															
O. (E.) sp. 5		15	F(%)	—	—	—	—	2	4	—	—	1	1	—	—	—
C/O sp. 51	11															
O. (E.) sp. 6		29	F(%)	5	2	1	1	—	2	—	—	—	—	—	4	2
C/O sp. 61	4		F(%)	—	4	—	—	—	—	—	—	—	—	—	—	3
O. (E.) sp. 7		27	F(%)	7	4	—	—	—	—	—	—	—	1	—	16	16

TABLE 1 (con't)

Taxon	Frequency (# collec- tions)	Total # Collected		Data by Month 1	2	3	4	5	6	7	8	9	10	11	12	Other Data
Diplocladius cultriger	20	364	N̄	2.5	0.1	—	—	—	—	—	—	—	—	0.9	2.2	
Epoicocladius sp.	2	4	F(%)	—	—	2	—	—	6	—	—	—	—	—	—	
Eukiefferiella			F(%)	41	19	21	29	27	25	3	15	21	16	15	14	
brevicalcar gr. (2)	206	1663	N̄	1.8	0.4	0.5	1.2	0.8	1.5	0.3	0.8	1.3	8.1	2.8	0.5	
			F(%)	13	4	13	16	6	19	—	2	12	2	—	7	
E. claripennis gr. (4)	86	337	N̄	0.5	0.1	0.3	1.0	0.1	0.5	—	0.1	0.6	0.1	—	0.5	
			F(%)	15	4	14	3	11	7	—	4	14	2	—	14	
E. brehmi gr. (1)	74	278	N̄	0.6	—	0.5	0.1	0.2	0.2	—	0.1	0.9	—	—	0.8	
			F(%)	11	12	9	16	11	11	10	9	23	14	4	21	
E. devonica gr. (2)	121	1410	N̄	0.6	0.4	0.2	1.1	1.0	2.6	0.3	1.5	2.1	3.7	0.2	1.4	
E. pothastia gr. (2)	9	54	F(%)	—	—	—	—	—	—	—	—	—	1	—	14	
E. pseudomontana gr. (1)	—	—	F(%)	—	—	—	—	—	—	—	—	—	—	—	—	X
Georthocladius sp.	—	—	F(%)	—	—	—	—	—	—	—	—	—	—	—	—	X
Genus nr. Heleniella	3	6	F(%)	—	—	—	2	—	—	—	—	—	—	—	—	
Genus nr. Nanocladius A	7	52	F(%)	5	—	—	2	—	—	—	—	1	2	—	—	
Genus nr. Nanocladius B	—	—	F(%)	—	—	—	1	2	—	—	2	—	—	—	—	
Heleniella sp.	8	11	F(%)	1	—	—	1	2	—	—	1	1	1	—	2	
Heterotrissocladius sp.	2	10	F(%)	—	—	—	—	2	—	—	—	1	—	—	2	
Hydrobaenus spp.	4	4	F(%)	—	2	—	—	2	—	—	—	—	—	—	2	
Krenosmittia sp.	—	—	F(%)	—	—	•	—	—	—	—	—	—	—	—	—	X
Limophyes spp. (3+)	17	34	F(%)	3	—	7	2	2	3	—	1	—	—	—	2	

Taxon			Type													
Lopescladius sp. (= "Cordites")	13	39	F(%)	—	—	1	—	1	—	8	3	—	2	—	—	X
Metriocnemus sp.	1	1	F(%)	—	—	—	—	—	—	—	—	—	—	—	2	
M. nr. fuscipes	—	—	F(%)	—	—	—	—	—	—	—	—	—	—	—	—	
Nanocladius spp. (3)	24	87	F(%)	1	—	1	1	5	2	3	3	5	—	—	9	
N. nr. balticus	2	2	F(%)	—	—	1	1	—	1	—	—	—	—	3	3	
N. downesi	8	57	F(%)	36	25	21	6	3	1	10	9	26	21	19	41	
Parachaetocladius sp. 1	59	845	N̄	3.0	0.9	0.7	0.1	—	0.1	0.1	0.2	1.1	1.2	0.9	3.5	
Paracricotopus sp.	5	10	F(%)	—	—	—	1	—	1	—	2	—	1	—	—	
Paraphaenocladius/	—	—	F(%)	58	42	38	42	32	44	33	22	47	27	42	59	
Parametriocnemus	370	3335	N̄	6.1	10.6	0.8	3.3	5.0	1.6	0.7	0.9	2.7	1.5	16.1	6.9	
sp. 1 (= lundbecki?)	17	23	F(%)	1	—	5	2	—	—	10	1	5	—	—	—	
P. sp. 2	4	14	F(%)	—	—	1	1	3	1	—	—	—	—	—	—	
P. sp. 3	4	35	F(%)	1	—	1	2	—	—	—	—	—	—	—	—	
Parakiefferiella sp. 1	1	—	F(%)	—	2	—	—	—	—	—	—	—	—	—	—	
P. nr. triquetra	16	31	F(%)	2	2	3	3	—	—	3	3	3	3	3	—	
Psectrocladius spp.	—	—	F(%)	—	—	3	3	11	4	17	13	3	7	—	—	X
P. cf. simulams	53	156	F(%)	—	—	3	3	—	1	—	1	1	1	—	2	
Rheocricotopus robacki	11	28	F(%)	—	2	1	4	—	1	—	1	1	—	—	3	
R. sp. 2	15	51	F(%)	3	—	5	3	3	—	—	—	3	—	—	3	
R. sp. 3	—	—	F(%)													
R. sp. 4	—	—	F(%)													X X
Rheosmittia nr. delicatula	1	1	F(%)	—	—	—	—	1	1	—	—	—	—	—	—	
Smittia sp.	1	19	F(%)	1	—	1	1	—	1	—	—	2	3	—	—	
Synorthocladius sp.	7		F(%)	5	—	3	3	17	16	17	21	37	24	8	14	

TABLE 1 (con't)

Taxon	Frequency (# collections)	Total # Collected		Data by Month 1	2	3	4	5	6	7	8	9	10	11	12	Other Data
Thienemaniella spp. (2+)	146	901	N	0.2	—	—	0.8	0.7	0.4	0.2	0.7	1.2	5.0	0.1	0.3	
			F(%)	39	13	21	20	48	46	33	18	22	28	38	47	
Tvetenia bavarica gr. (1)	280	4878	N	2.1	0.5	0.4	0.9	12.8	4.2	1.2	0.5	1.1	25.5	4.1	8.0	
			F(%)	23	6	15	18	17	34	27	17	34	28	31	17	
T. discoloripes gr. (1)	209	2697	N	1.5	0.2	0.6	•0.8	0.5	4.3	0.8	1.0	4.5	13.0	2.0	0.6	
Xylotopus par	3	4	F(%)	—	—	—	—	2	—	—	—	1	—	—	2	
Orthocladiinae type acutilabis	17	20	F(%)	—	—	4	—	—	4	7	2	4	1	—	—	
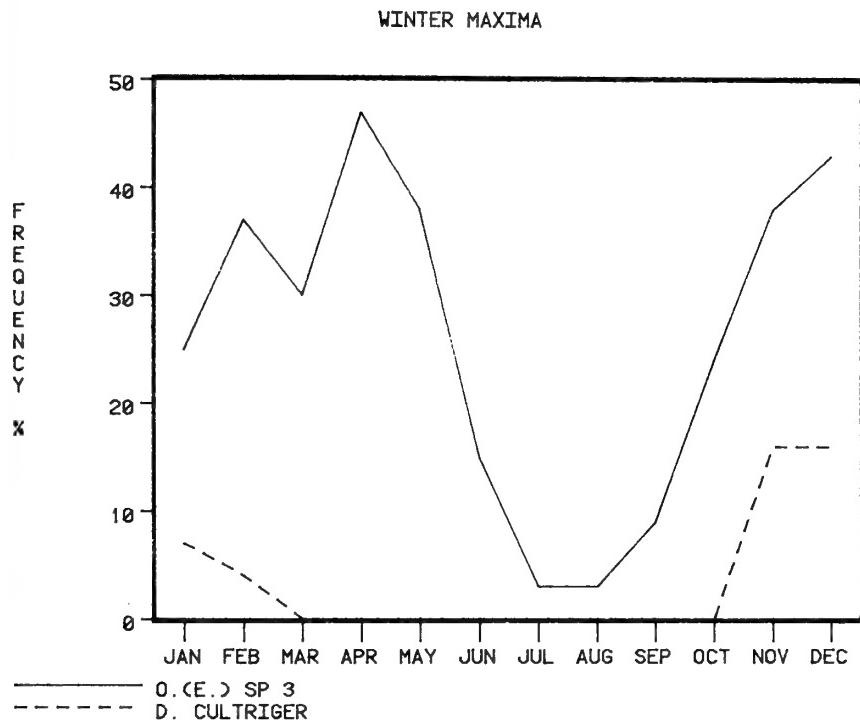
WINTER MAXIMA

FIG. 1.   Some chironomid species with winter maxima.

TABLE 2.   Approximate number of larval chironomid taxa collected in North Carolina freshwater lotic systems; DEM collections 1978-1982.

Group	Mountains		All N.C. Collections	
	#	%	#	%
Tanypodinae	16	10	28	12
Chironomini	38	23	56	24
Tarytarsini	14	8	21	9
Diamesinae	9	5	11	5
Orthocladiinae	91	54	117	50
Total	168	100	233	100

chironomid species prefer either streams (2nd order) or rivers (4th-5th order) within a single North Carolina watershed.

Chironomids may also avoid competition by means of temporal separation. Many examples may be drawn from Table 1. Fig. 5 illustrates the
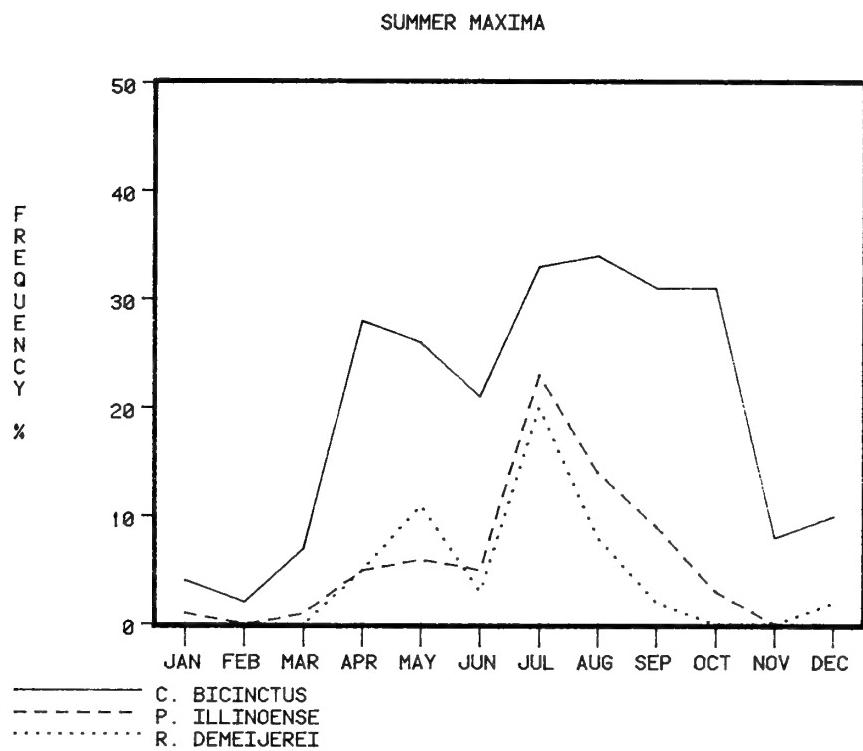
SUMMER MAXIMA

FIG. 2.   Some chironomid species with summer maxima.

TABLE 3.   Number of maxima (frequency data) classified by sub-
family and season.

| | Season | | |
Subfamily	Winter	Spring-Fall	Summer
Tanypodinae	1	1	1
Chironominae	6	8	16
Diamesinae	2	2	2
Orthocladiinae	18	23	13
TOTAL	26	33	31

seasonal distribution of the 5 most abundant *Polypedilum* species (from
Table 1). *Polypedilum convictum* gr. (includes P. *aviceps*) is a warm
eurythermal taxon that is common from April to October. The other less
common species show a distinct separation in the timing of the first spring

SPRING–FALL MAXIMA

C. VARIPES GR.
P. GAEDI
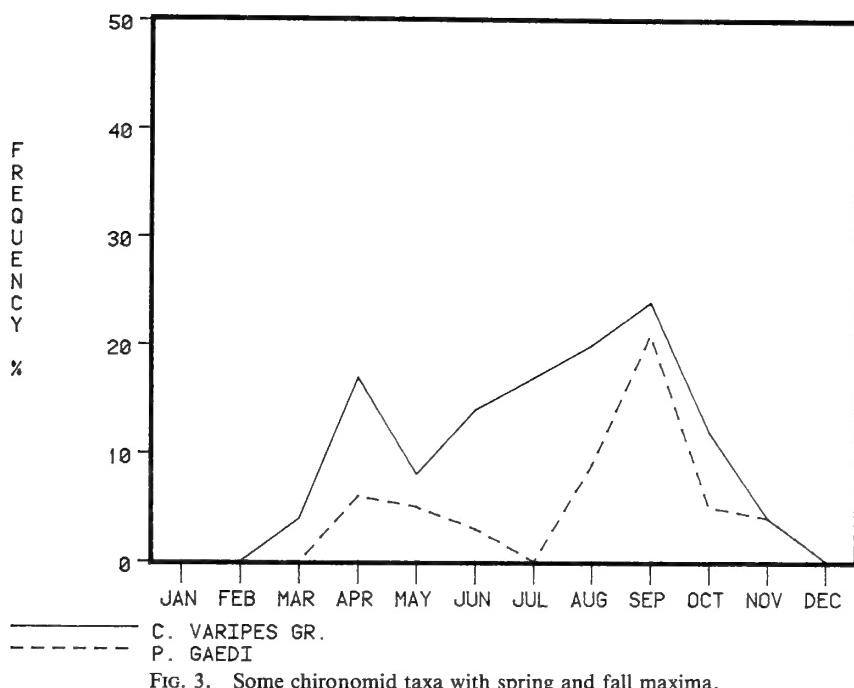
FIG. 3.   Some chironomid taxa with spring and fall maxima.

or summer peak; *Polypedilum angulum's* first peak occurs in March, followed by that of *P. fallax, P. halterale* and *P. illinoense.*

Fig. 6 illustrates the seasonal distribution of 3 *Cricotopus* taxa. As with the genus *Polypedilum,* there is one warm eurythermal species: *Cricotopus bincinctus.* This species has been studied in detail by other investigators, including Rosenberg *et al.* (1977) and LeSage and Harrison (1980). Data presented by these investigators suggests that the April peak represents a single spring generation, while the broad July-October peak represents another 3-4 summer generations. The other two *Cricotopus* species have spring-fall maxima. For both seasons the *C. varipes* gr. peak precedes the *C. infuscatus* gr. peak. A similar pattern is seen for *C. bicinctus* vs. *C. in-fuscatus* gr. Note that this type of succession is inconsistent with strict temperature control. The direct competition and territoriality observed by Wiley (1982) and Menzie (1978) between *Cricotopus* individuals may influence the timing of these peaks.

Seasonal niche division by chironomids may be seen not only at the genus level, but also at the family or subfamily level. Table 3 shows the number of

3-4 MAXIMA
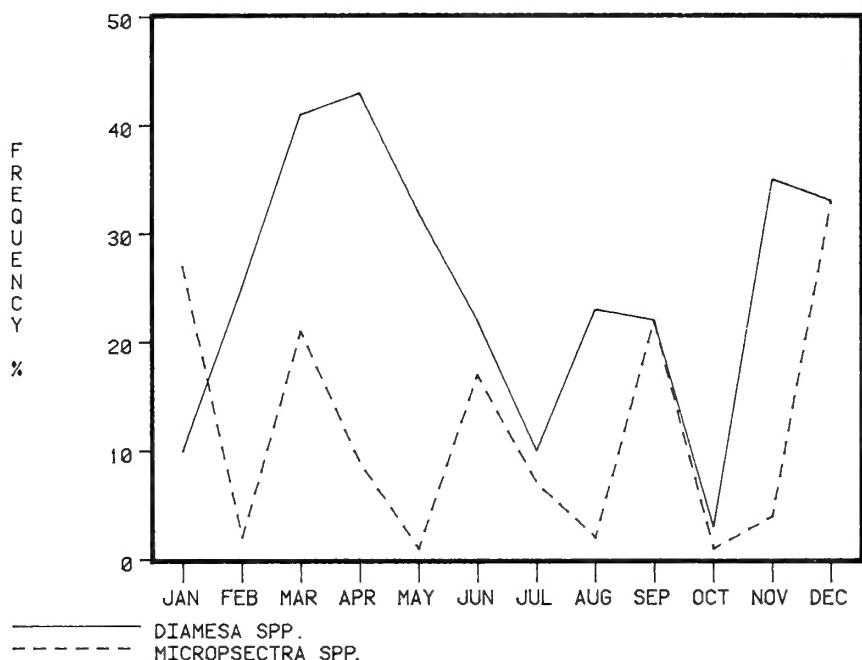
Fig. 4.   Some chironomid taxa with 3-4 seasonal maxima.

maxima occurring in winter, spring and/or fall and winter. Only the more abundant taxa are considered. The fairly even distribution among these three categories suggests a constant seasonal replacement. The breakdown by subfamily does not differ significantly between the winter and the spring-fall groups, but summer data shows a distinct shift from Orthocladiinae to Chironominae. Similar shifts have been shown by many others and Boerger (1981) suggests that this is the "general pattern in north temperate streams." From the point of view of the applied ecologist, it is important to separate this shift from similar charges associated with organic enrichment.

Other investigations in unstressed North Carolina mountain streams (Lenat, in manuscript) have indicated 2 seasonal peaks in average chironomid species richness/collection: winter (January), and fall (September-October). This type of seasonality can also be observed in Table 1 frequency data. To generate a composite seasonal curve for the entire chironomid community, we have calculated an average frequency value for each month (Fig. 7). The average frequency parameter is related to the rarity of chironomids and can be used to summarize the distribution of the

POLYPEDILUM SPP.
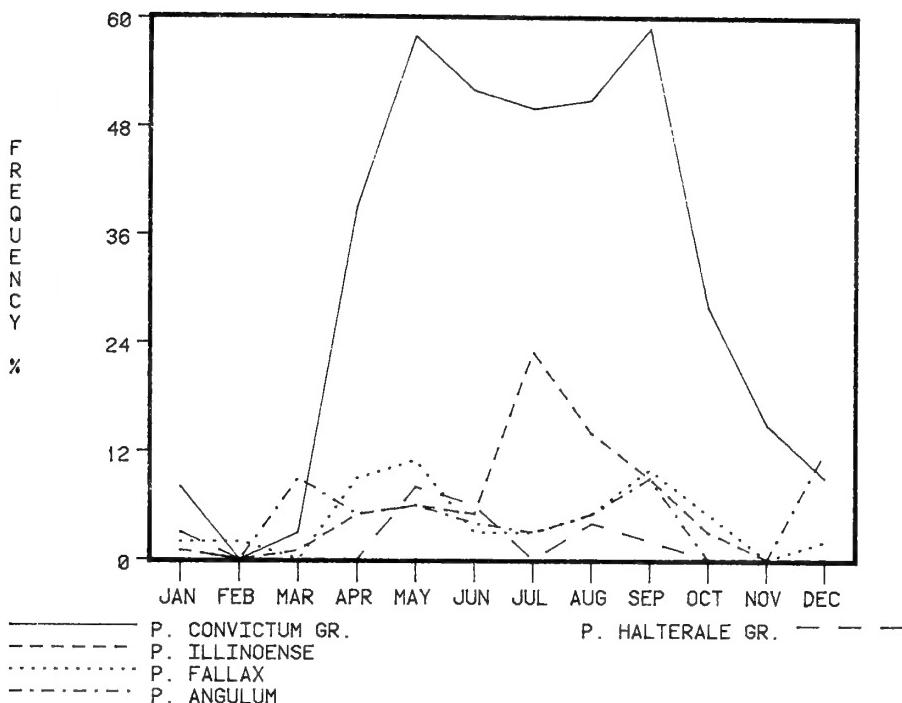
Fig. 5. Seasonal distribution of *Polypedilum* species.

community. Fig. 7 shows 3 peaks/year: winter (December-January), spring (May-June) and fall (September). This pattern is very similar to the previously described seasonal distribution of chironomid species richness.

Seasonal changes in chironomid rarity may be partially due to changes in abundance (Figure 7). Like average frequency, average number/sample (abundance) had 3 seasonal peaks, but these peaks generally lag one month behind frequency peaks. Note that abundance values are mostly strongly affected by older (especially 4th instar) individuals; this accounts for the lag between frequency and abundance. The absence of a lag during the spring period is attributed to the overlapping influence of spring and summer species.

It is important to recognize the presence of seasonal variation in chironomid rarity or species richness, so that natural seasonality can be differentiated from the effects of pollution. We speculate that such seasonal variation could be caused by a difference in the environmental cues that

CRICOTOPUS SPP.

C. BICINCTUS
C. INFUSCATUS GR
C. VARIPES GR.
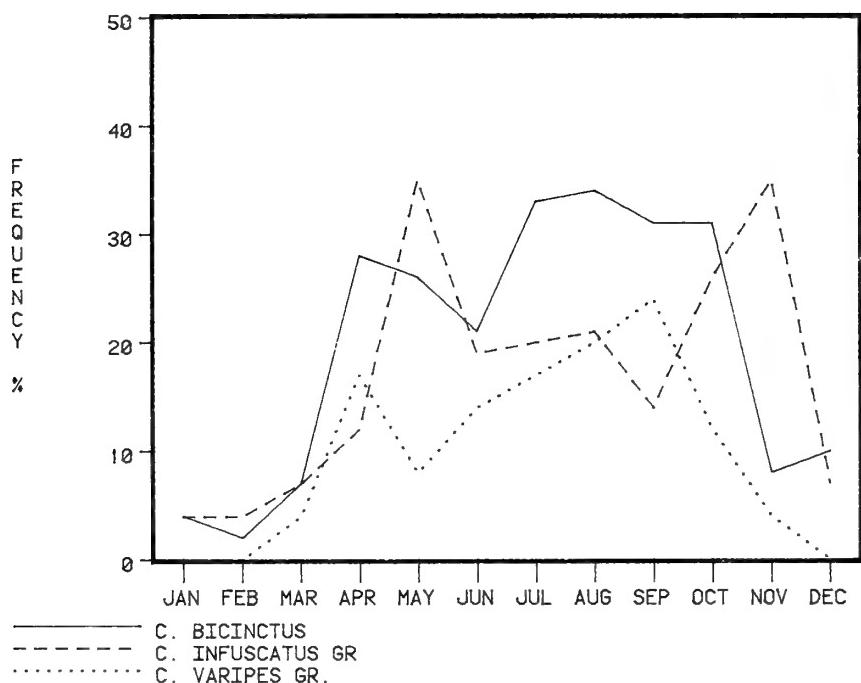
FIG. 6.   Seasonal distribution of *Cricotopus* species.

stimulate emergence of one generation and growth of the following genera-
tion. For example, the seasonal minimum observed in February could be ex-
plained by a lag between emergence of winter generations and development
of spring generations cued by rising water temperatures in March. The most
intensively studied chironomid community is that of Linesville Creek, a
third order stream in Pennsylvania (Coffman 1973). There are several
parallels between data from North Carolina and Linesville Creek. Coffman
(1973) found peak emergence in May and September, corresponding with
our spring and fall frequency maxima. He also records a minimum in late
June and July attributed to a gap between the first and second summer
generation. One distinct difference between Linesville Creek and North
Carolina streams is the presence of a winter generation in North Carolina,
possibly due to warmer winter water temperatures.

Average Frequency/Abundance
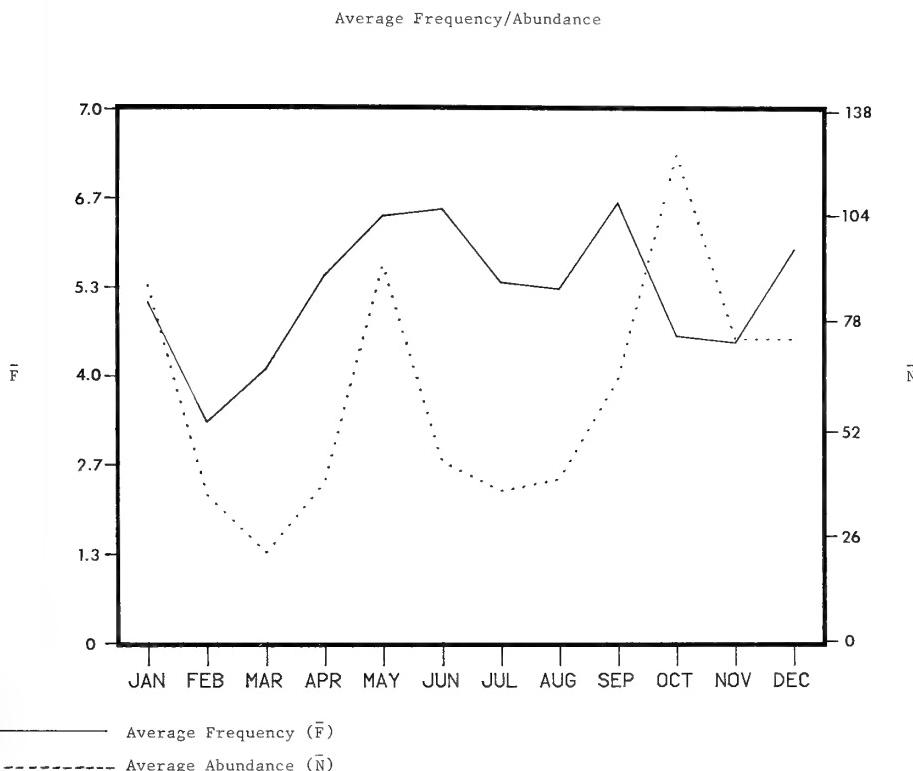
FIG. 7. Seasonal distribution of chironomid rarity.

REFERENCES

AAGAARD, K. 1978. The chironomids of Lake Målsjøen. A phenological, diversity and production study. Norw. J. Ent. 25:21-37.

BOERGER, H. 1981. Species composition, abundance and emergence phenology of midges (Diptera: Chironomidae) in a brown water stream of West-Central Alberta, Canada. Hydrobiologia 80:7-30.

COFFMAN, W.P. 1973. Energy flow in a woodland stream ecosystem: II. The taxonomic composition and phenology of the Chironomidae as determined by the collection of pupal exaviae. Arch. Hydrobiol. 71:281-322.

FROST, S., A. HUNI AND W.E. KERSHAW. 1971. Evaluation of a kicking technique for sampling stream bottom faura. Can. J. Zool. 49:167-173.

GURTZ, M.E. 1981. Ecology of stream invertebrates in a forested and a commercially clear-cut watershed. Ph.D. Dissertation, Univ. Georgia, 148 pp.

HUTCHINSON, G.E. 1961. The paradox of the plankton. Amer. Natur. 95:137-145.

JANKOVIC, M.J. 1979. Communities of chironomids in the Velika Morava River, Hydrobiologia 64:167-173.

LESAGE, L. AND A.D. HARRISON.   1980.   The biology of *Cricotopus* (Chironomidae: Ortho-
cladiinae) in an algal-enriched stream = Part I. Normal biology. Arch. Hydrobiol./
Suppl. 57:375-418.

LINDEGAARD-PETERSEN, C.   1972.   An ecological investigation of the Chironomidae (Dip-
tera) from a Danish lowland stream (Linding Å). Arch. Hydrobiol. 69:465-507.

MAKARERICZ, J.C. AND G.E. LIDENS.   1975.   Niche Analysis of a zooplankton community.
Science 190:1000-1003.

MENZIE, C.A.   1978.   Productivity of chironomid larvae in a littoral area of the Hudson
River Estuary. Ph.D. Dissertation, City Univ. N.Y., 150 pp.

PENROSE, D.L., D.R. LENAT AND K.W. EAGLESON.   1983.   Aquatic macroinvertebrates of
the Upper French Broad River Basin. Brimleyana, 8:27-50.

POLLARD, J.E. AND W.L. KINNEY.   1979.   Assessment of macroinvertebrate monitoring
techniques in an energy development area: A test of the efficiency of three
macroinvertebrate sampling methods in the White River.

RAMCHARAN, V. AND C.G. PATTERSON.   1978.   A partial analysis of ecological segregation in
the chironomid community of a bog lake. Hydrobiologia 58:129-135.

ROSENBERG, D.M., A.P. WIENS AND O.A. SAETHER.   1977.   Life histories of *Cricotopus*
(*Cricotopus*) *bicinctus* and *C. (C.) mackenziensis* (Diptera: Chironomidae) in the Fort
Simpson Area, Northwest Territories. J. Fish. Res. Board Can. 34:247-253.

WILEY, M.J.   1981.   Interacting influences of density and preference on the emigration rates
of some lotic chironomic larvae (Diptera: Chironomidae). Ecology 62:426-438.

Terminology of the Wing-Veins in Chironomidae (Diptera)

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ABSTRACT. — It is suggested that the Comstock-Needham reference system can still be used in the taxonomy of the Chironomidae, with some minor additions and corrections. The veins of the radial sector are impossible to be homologized for the time being. M_3 or its vestige is obviously present, and can be added to the list of terms. Arguments are presented for using Cu_1 (or eventually CuA_1) instead of M_{3+4} or M_4. The presence of CuP is discussed. It is proposed that the term claval furrow can be applied, but the term vannal fold should be discarded.

INTRODUCTION

Over 15 years ago (Lindeberg 1964, 1966), I tried to identify the wing-veins of the Chironomidae, and certain other families of nematocerous Diptera. The outcome was one new explanation and several indefinite suggestions. Furthermore, I proposed that in practical taxonomy the traditional system of Comstock and Needham should be applied.

The most confident result was the interpretation of the tanypodine R_1. "R_1", "R_2", and "R_3" are all parts of one vein, R_1. I am using quotation marks to indicate the traditional abbreviations. Fittkau (1965) promptly accepted the idea and presented additional evidence in favor of my suggestion.

The basalization and disappearance of the original posterior basal cell (cf. Tanyderidae, Psychodidae, Simuliidae) was thought to be responsible for the structure between "M" and "Cu", probably the vestige of M_3. I still think that such a development may have taken place. The naming of the veins of the radial sector was very hypothetical.

DISCUSSION

Since we have the elaborate plan of Hennig (1969) covering not only the Diptera but all the winged insects, it is no longer a question whether to apply the Comstock-Needham system or the Tillyard modification. If a uniform system is to be strived for, then Hennig's results cannot be disregarded. It is highly likely that disagreements will continue and new suggestions will appear at times. Hennig (1969, p. 385) frankly admitted that in his system there are hypotheses that could neither be proved nor disproved.

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Radius. — An example of the difficulties in interpretation are the veins of the radial sector. "R_2" of the Tanypodinae, actually a part of R_1, is R_{2+3} by Hennig. Consequently, "R_{2+3}" and "R_{4+5}" are R_4 and R_5, respectively. But these veins can also be interpreted as R_2 and R_3, as is the usage in Simuliidae taxonomy. The only alternative is to continue with the traditional terms "R_{2+3}" and "R_{4+5}". For the Tanypodinae, too, the traditional system can be applied. Fittkau continues to use the traditional nomenclature, although he has accepted another morphological explanation.

Media. — According to Hennig, "M" is M_{1+2}. Hansen & Cook (1976) and Saether (1980) follow this naming. I have suggested that "M" is not a fusion product, but that M_2 has been reduced in the Chironomidae. However, this vein could be named M_1 because there is a concave structure between "M" and the cubitus. It is indicated in many illustrations of chironomid wings. If my hypothesis of the basalization and disappearance of the posterior basal cell holds true, then it really could be M_3. In any case, I need a name for it, since there are differences in the trichation of this structure between closely related species. Figure 1 shows the wings of *Constempellina brevicosta* (top) and two undescribed species. Adding M_3 to the traditional system would create no confusion.

Media-Cubitus Crossvein. — MCu (Saether, 1980) or traditionally "m-cu" is not an original crossvein or the base of M_{3+4} present in many other Diptera families. It is the track of a trachea leaving the trunk of the cubitus and joining the media. This idea was supported by Hansen & Cook (1976:38), ". . . Lindeberg's (1964) suggestion that this so-called m-cu is actually a secondarily acquired cross-vein seems reasonable . . ."

Cubitus. — The name for the anterior branch of the cubital fork is different in the Comstock-Needham system (Cu_1) and the Tillyard modification (M_{3+4}). Hennig (1969) supports the idea that "Cu_1" is a fusion of M_4 and CuA_1, but he always abbreviated it M_4. The complete name, $M_4 + CuA_1$, is really too long to be practical.

There is, however, no need to apply M_4 or M_{3+4} to the anterior branch, because it is formed of a medial and cubital element. It remains to chose between two alternatives. The cubital element is dominating as the vein is distinctly convex. Therefore, it can be named as before. More recent authors, Soponis (1977) and Pinder (1978) have continued with the traditional usage. It would be more precise to follow Séguy (1959) and Hennig (1969) in writing CuA_1 and CuA_2, but I do not think this is necessary.

Hennig (1969) stated that the posterior cubitus (CuP) is rudimentary or lacking in Diptera, but I have seen it well developed in several families. It is a strongly concave vein that often lies deep under the stem of CuA. To
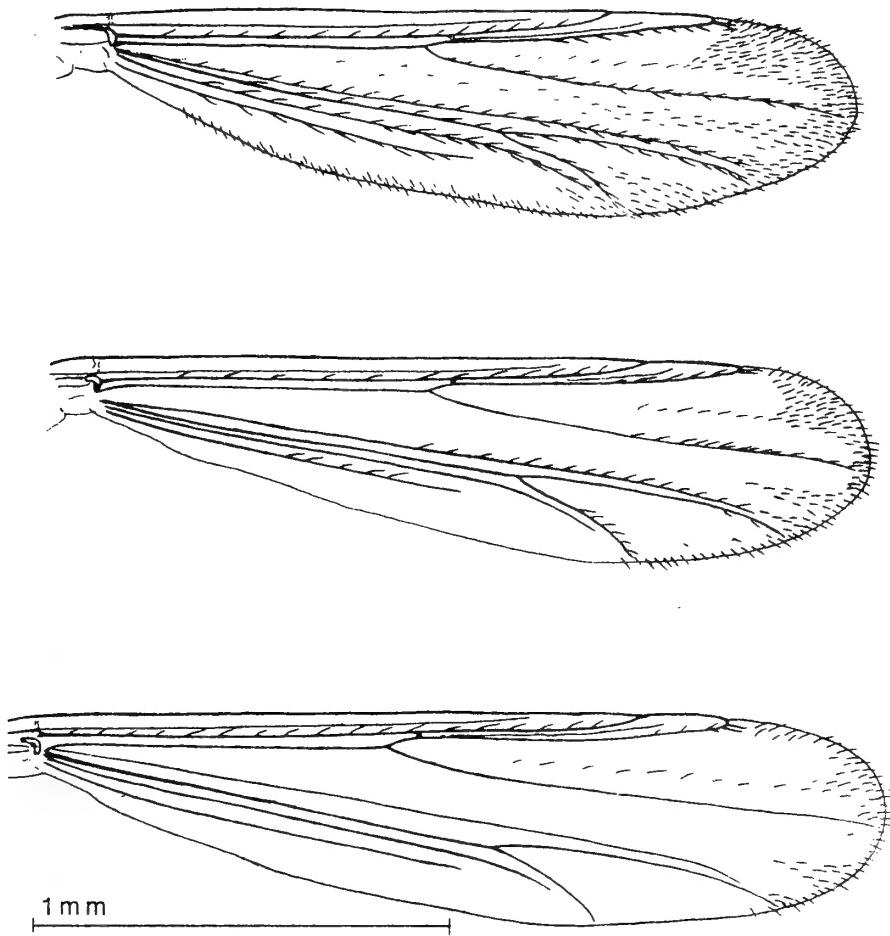
FIG. 1. Wings of *Constempellina brevicosta* (top) and two new closely related species (unpublished). Border fringe of setae omitted. Note the differences in the distribution of setae in the cells, and on the veins, particularly M_3, CuP, and An.

observe it, one must examine the wing from below. In the Chironomidae it is usually visible from above, its base may be strongly sclerotized, and it is indicated in all good illustration of the wing. It is undoubtedly the posterior cubitus (CuP) and can be introduced into the chironomid terminology. I will be using it shortly because there are differences in the trichation of this vein in *Constempellina brevicosta* and two other closely related species (Fig. 1).

For the Chironomidae, Hansen and Cook (1976) introduced a new term, the vannal fold. It is in the same position as the above CuP. Saether (1980) also uses this term. In the first place, I think it is a vein. Secondly, Wootton (1979) has remarked that Snodgrass confused the vannal fold with the claval furrow. Vannal fold refers to a fold of the anal fan of the hind wing only.

Clavus. — After the posterior cubitus (CuP) comes a convex vein, although there are no problems about it for it is the first anal vein. In large Chironomini, with a broad wing-base there is a distinct ridge in the anal lobe, but so far I have not seen any vein structures. It may be the vestige of the second anal vein. Between these two, there is a straight furrow in many larger species, such as *Chironomus* and *Protanypus*. It cannot be seen in small species such as *Constempellina* spp. with the wings narrow at the base. This may be the true claval furrow, a longitudinal flexion-line for aerodynamic functions. Wootton (1979) stated that the claval furrow is usually between CuP and An_1, but the Diptera seem to be an exception. My few observations support the idea that in the Chironomidae it lies posterior to An_1.

LITERATURE CITED

FITTKAU, E.J. 1965. Veranderungen des Flugelgeaders bei Tanypodine (Diptera Chironomidae) im Verlauf der Evolution. Proc. 12th Int. Congr. Entomol., London. pp. 70-71.

HANSEN, D.C. AND E.F. COOK. 1976. The systematics and morphology of the nearctic species of *Diamesa* Meigen, 1835 (Diptera: Chironomidae). Mem. Amer. Entomol. Soc. 30:1-203.

HENNIG, W. 1969. Die Stammesgeschichte der Insekten. Verl. Kramer, Frankfurt. 436 pp.

LINDEBERG, B. 1964. Nomenclature of the wing-venation of the Chironomidae and of some other families of the nematocerous Diptera. Ann. Zool. Fenn. 1:147-152.

_____. 1966. Das Flugelgeader der Chironomiden. Gewasser Abwasser 41/42: 44-47.

PINDER, L.C.V. 1978. A key to the adult males of the British Chironomidae (Diptera). Freshw. Biol. Assoc., Sci. Publ. 37(1):1-169.

SAETHER, O.A. 1980. Glossary of chironomid morphology terminology. Entomol. Scand., Suppl. 14:1-51.

SÉGUY, E. 1959. Introduction a l'étude morphologique de l'aile des insectes. Mém. Mus. Nation. Hist. Nat., Sér. A 21:1-248.

SOPONIS, A.R. 1977. A revision of the Nearctic species of *Orthocladius (Orthocladius)* van der Wulp (Diptera: Chironomidae). Mem. Entomol. Soc. Canada 102:1-187.

WOOTTON, R.J. 1979. Function, homology and terminology in insect wings. Syst. Entomol. 4:81-93.

Succession of Chironomidae (Diptera) in Hjarbæk Fjord, Denmark, during a Period with Change from Brackish water to Freshwater[1]

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ABSTRACT. — Hjarbæk Fjord (24.8 km^2, z_{max} = 6.5 m, $\bar{z}$ = 1.9 m) was cut off from the sea by a dam in 1966. Within a few years, the surface salinity decreased from 7-19 o/oo to less than 1 o/oo. Less than 10% of the area of Hjarbæk Fjord is deeper than 3 m. This contains stratified water with salinities up to 5 o/oo. A typical *Macoma baltica* community existed before 1966, probably including chironomids such as *Chironomus salinarius* and *C. halophilus*. Samples collected in 1968, 1971, 1973, 1976-77 and 1981 showed a change to a freshwater community characterized by *Chironomus plumosus* f. *semireductus*, *Cryptochironomus redekei*, *Polypedilum bicrenatum*, *P. nubeculosum* and *Cladotanytarsus* spp. *Fleuria lacustris* appeared between 1973 and 1976 and has since increased in number. Colonization by chironomids began in proximity to 4 large inlets; by 1971 they were common over extensive areas of the lake. Heavy nutrient input increased the chironomid density from 3,000-4,000 ind. m^{-2} in 1971-73 to approximately 32,000 in 1981, the latter representing 95% of the total benthic fauna. About 20 km^2 of Hjarbæk Fjord provide a suitable habitat for chironomids, which have been a nuisance to residents since 1975. The problem is enhanced by the specific behaviour of *Fleuria lacustris*.

INTRODUCTION

Whereas there have been frequent reports of colonization by Chironomidae in newly constructed reservoirs (e.g., Nursall 1952, Morduchai-Boltovskoi 1961, Paterson and Fernando 1970, McLachlan 1974), there have been comparatively few studies undertaken in brackish waters cut off from the sea to form freshwater lakes (Lenz 1933, Havinga 1941). One such example is IJsselmeer in the Netherlands where midges have been a nuisance (Kruseman 1935, v.d. Torren 1939).

Hjarbæk Fjord, Denmark, was in 1966 cut off from the sea by a dam, which resulted in a rapid decrease in salinity. This corresponded with an increase in nutrients and concurrent high phytoplankton production, providing ideal conditions for growth of chironomids which have become a serious nuisance to local residents over the last five years. Comprehensive studies on Hjarbæk Fjord were therefore undertaken in 1980 and 1981.

These showed a.o. an unusual species composition of the chironomid community and densities of 32,000 larvae per m². Samples of bottom fauna from previous surveys, to quantify food available for ducks in 1968, 1971, 1973 and 1976/77 (Jepsen 1976, Christensen 1979) were reexamined in the light of the present study to help determine the development of the chironomid community during the transition period of the lake. Production and population dynamics of the dominating species, from April 1981 to May 1982, are given elsewhere (Lindegaard and Jónsson, in prep).

STUDY AREA

Hjarbæk Fjord (56° 34′ N, 9° 17′ E) covers an area of 24.8 km². Maximum depth is 6.5 m, but over 90% of the lake is shallower than 3 m, giving an average depth of 1.9 m (Fig. 1). Before 1966, the "lake" was connected to the brackish Limfjord by a 200 m narrow strait. This communication was removed by the construction of a dam, and a sluice gate now prevents intrusion of brackish water from the Limfjord. The dam construction resulted in reduced salinity; from 7-19 o/oo to less than 1 o/oo at present. A limited area (1.5 km ²) close to the sluice gate contains bottom water of higher salinity (up to 5 o/oo, which is isolated from the outflowing freshwater by a stable chemocline.

Four large tributaries provide most of the water input to the lake, giving a renewal time of about 7 weeks. Sewage and agricultural runoff result in maximum concentrations of total phosphorus and total nitrogen of 800 and 5000 μg l^{-1}, respectively. An increase in phytoplankton production was evident following the establishment of the dam. Phytoplankton production was estimated in 1959 to be about 50 g C m^{-2} yr^{-1} (Grøntved 1960), and in both 1974 and 1981 at approximately 400 to 500 g C m^{-2} yr^{-1}. Water transparency was typically about 0.4 m during the summer. However, in the late summer of 1980 and 1981 higher transparencies (1 m) were measured, presumably due to grazing of the phytoplankton by large populations of *Daphnia hyalina* Leydig. The latter occurred during a fish emigration (or kill) following high ammonium (NH$_4^+$) concentrations and pH levels (10.5-11.0) in the lake.

Dissolved oxygen is typically above 100% saturation throughout the water column, though it may fall below 30% saturation during windless periods. The saline bottom water, close to the sluice gate, is usually anoxic.

MATERIAL AND METHODS

In 1968, 1971 and 1973 the bottom fauna was sampled once each year with an Ekman dredge (area 225 cm²) to estimate available food for ducks
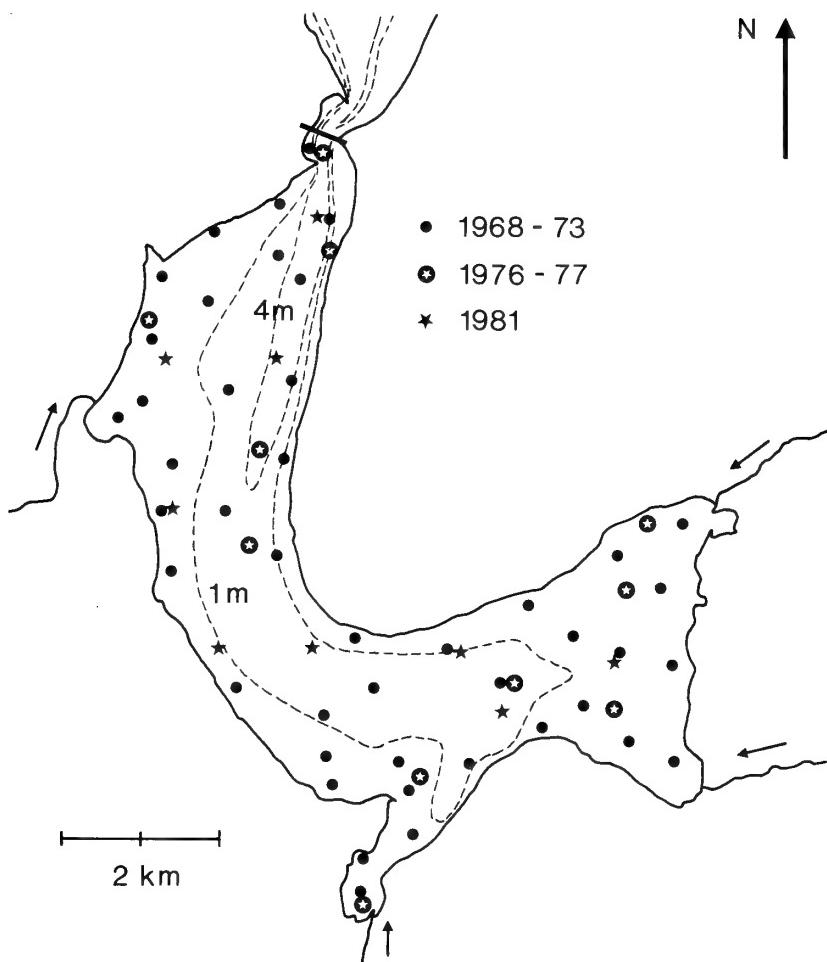
FIG. 1.   Hjarbæk Fjord showing the sampling stations and depth contours.

(Jepsen 1976, 1978). Core samples (area 20 cm²) were used both in 1976 to 1977 (Christensen 1979) and in 1981. Sampling frequency and mesh size of the sieves used are given in Table 1, and sampling sites are shown in Fig. 1. The heterogeneity of the material from 1968 to 1981 has been taken into account in presenting the results. In order to properly identify chironomid species, adults were taken in 1981 and 1982.

TABLE 1.   Sampling methods and efficiency in Hjarbæk Fjord during 1968-81.

	1968	1971	1973	1976-77	1981
Number of stations	28	40	26	11	9
Number of samples per station	1	1	1	5	5
Sampling frequency	1	1	1	3	8
Sample size (cm²)	225	225	225	20	20
Sieve mesh size (μm)	1000	1000	1000	200	225

TABLE 2.   List of Chironomidae found in Hjarbæk Fjord.

	larva	adult
Tanypodinae		
Procladius sp.	x	x
Psilotanypus sp.	x	
Orthocladiinae		
Cricotopus sylvestris (Fabr.)		x
Psectrocladius sp.	x	
Limnophyes globifer Lundstr.		x
Limnophyes sp. cfr. *minimus* (Mg.)		x
Metriocnemus hygropetricus Kief.		x
Corynoneura sp.	x	x
Thienemanniella sp.		x
Chironominae		
Camptochironomus tentans Fabr.		x
Chironomus plumosus L.		
f. *semireductus* Lenz	x	x
Chironomus salinarius Kief.		x
Cryptochironomus redekei Krus.	x	x
Dicrotendipes pulsus (Walk.)		x
Fleuria lacustris Kief.	x	x
Glyptotendipes sp.	x	
Polypedilum bicrenatum Kief.	x	x
Polypedilum nubeculosum (Mg.)	x	x
Stictochironomus histrio (Fabr.)		x
Cladotanytarsus spp.	x	x
Tanytarsus gracilentus Holmgr.	} x	x
Tanytarsus lestagei gr.		x

RESULTS

The 1981 community. — The survey in 1981 gave an average chironomid larvae density of 32,000 per m^2, representing 95% of the benthic fauna. The remaining 5% was mainly tubificids (Table 3). Chironominae species, able to withstand occasionally low oxygen concentrations, were the dominating elements of the community. The subfamily Orthocladiinae were represented only by a *Psectrocladius* species found in very low numbers, whereas in shallow water (< 0.5 m) *Corynoneura* and *Cricotopus* species were common. One or two species of *Procladius* and *Psilotanypus* (subf. Tanypodinae) together with *Cryptochironomus redekei* were the most important carnivorous invertebrates. At less than 0.5 m depth *Herpobdella octoculata* L. (Hirudinea) was a common predator.

Twenty-two chironomid taxa were recorded (Table 2), of which 7 contributed more than 99% of all larvae sampled. These were *Procladius* spp., *Chironomus plumosus* f. *semireductus, Cryptochironomus redekei, Fleuria lacustris, Polypedilum bicrenatum, P. nubeculosum* and *Cladotanytarsus* spp. With the exception of *Fleuria lacustris* all are common inhabitants of lakes. The above species are all known from brackish water (Fittkau and Reiss 1978), where some of them can develop large populations (Lenz 1954-62, Thienemann 1954).

The community from 1966 to 1981. — Data for the bottom fauna in Hjarbæk Fjord before the dam was built are not available. Description of the invertebrate communities in a number of similar localities in Denmark (Muus 1967) suggests a typical *Macoma baltica* community in Hjarbæk Fjord before 1966, dominated by mussels (*Mytilus, Cardium, Macoma, Mya*), snails (*Littorina, Hydrobia*), crustaceans (*Corophium, Idothea, Gammarus*) and polychaets (*Nereis*). Subfossil shells in bottom samples from 1968 to 1981 were consistent with this description. Chironomids belonging to either the *Chironomus salinarius* group or *Ch. halophilus* group are well known inhabitants of brackish water in Denmark (Andersen 1949, Muus 1967). Adults of *Ch. salinarius* have been found at Hjarbæk Fjord (Table 2).

The *Macoma baltica* community died soon after the establishment of the dam. Only a small population of *Hydrobia* spp. survived until 1968, when the snails *Potamopyrgus jenkensi* Smith and *Lymnaea pereger* Müller and the trichopteran *Oecetis ochracea* Curtis were numerous. In 1971, *P. jenkensi* had almost disappeared, while the densities of both *L. pereger* and *O. ochracea* had increased. Already in 1973 their density had declined and in 1976 and 1977 they were found scattered only in the shallow water (Jepsen 1976, Christensen 1979).
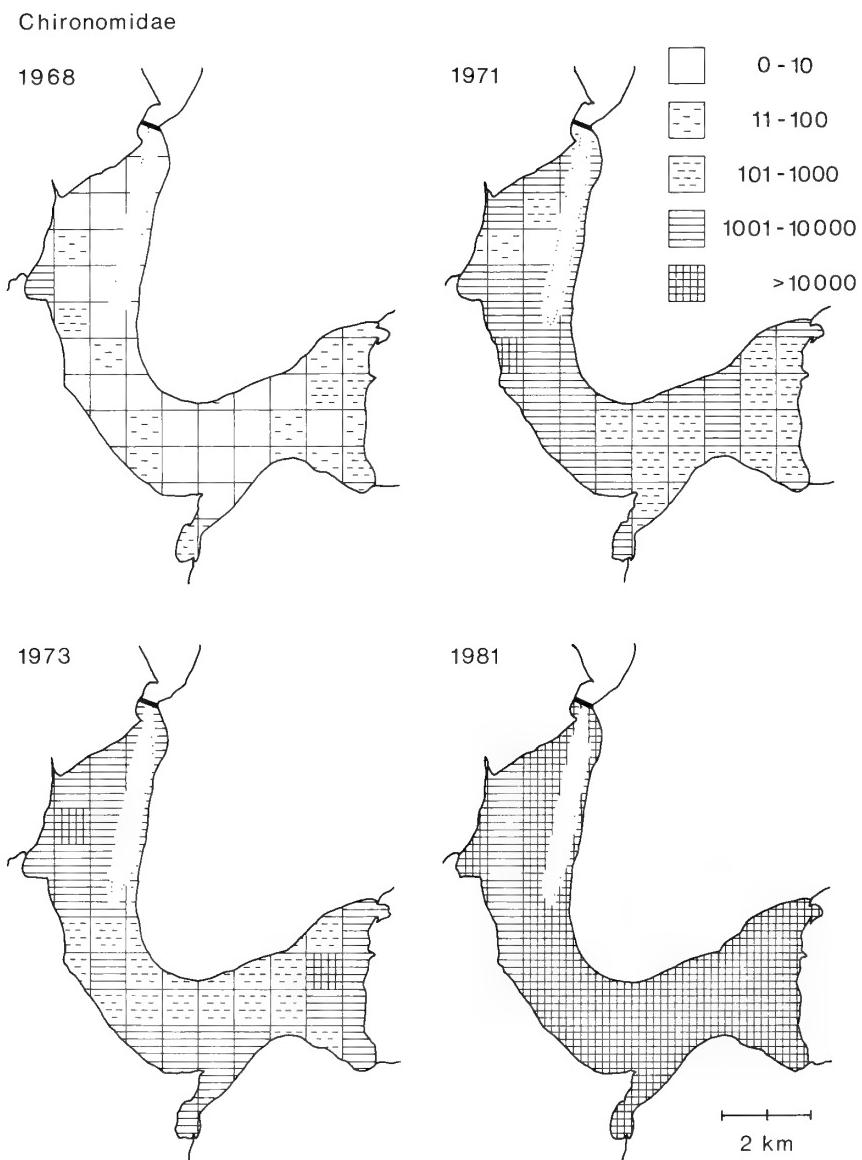
Chironomidae

FIG. 2.   Distribution of Chironomidae in Hjarbæk Fjord during 1968-81. Density in nos. m^{-2}.

Procladius sp.
1968

1971

0 - 10

11 - 100

101 - 1000

1001 - 10 000

> 10 000

1973

1981

2 km
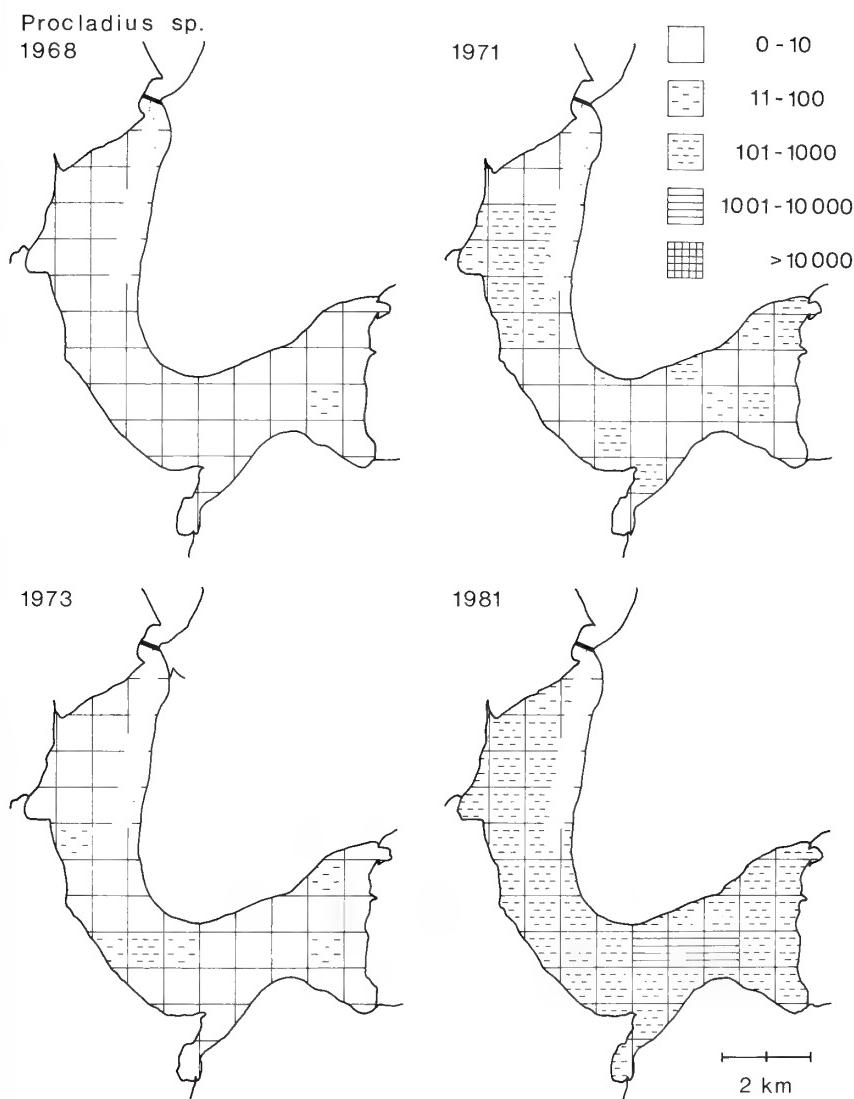
FIG. 3.   Distribution of *Procladius* sp. in Hjarbæk Fjord during 1968-81. Density in nos.
m⁻².

Densities of oligochaets showed wide fluctuations over the transition
period of the lake (Table 3). No species identification of oligochaets has
been made, but these fluctuations may be due to changes in species com-
position.

Chironomus plumosus f. semireductus
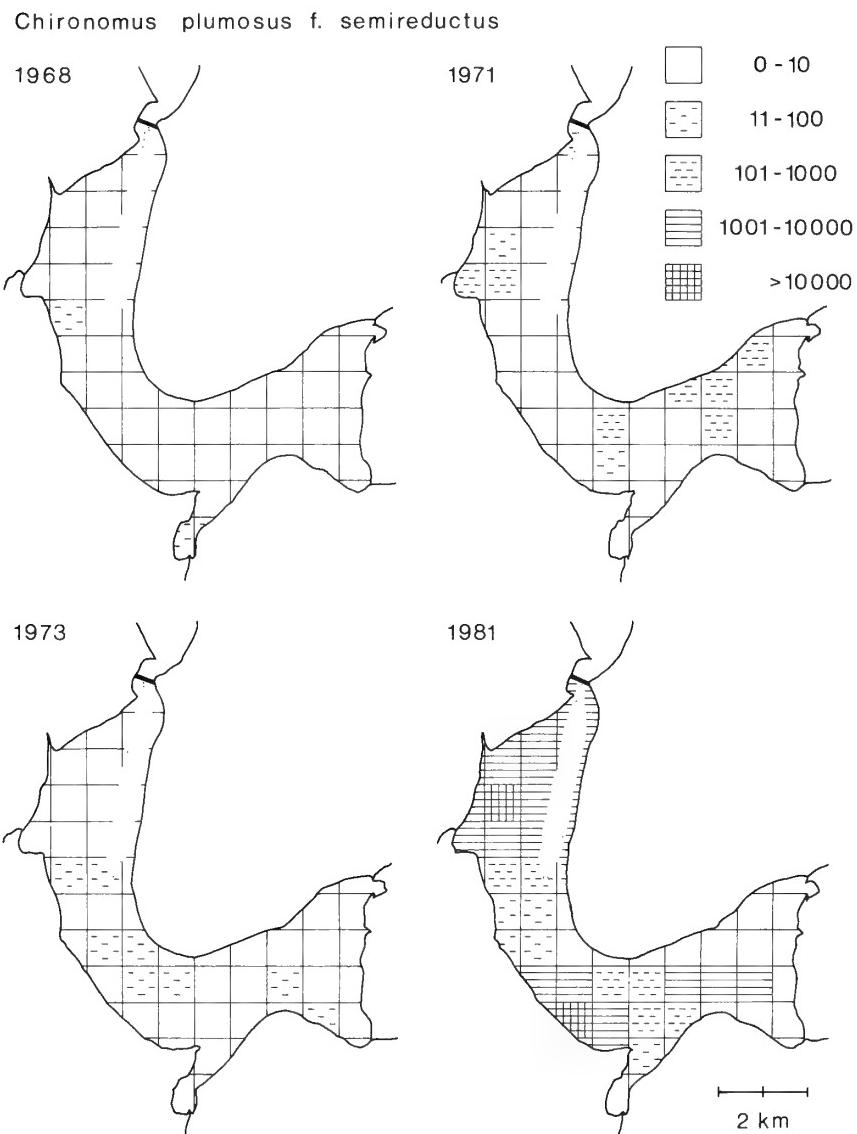
FIG. 4. Distribution of *Chironomus plumosus* f. *semireductus* in Hjarbæk Fjord during 1968-81. Density in nos. m^{-2}.

Changes in the chironomid community between 1968 and 1981 are given in Table 3 and Figs. 2 to 8. It appears that the average number of chironomid larvae per m^2 was only about 100 in 1968, but rose to 3,000 to

4,000 in 1971 and 1973. The larval densities increased further to some 19,000 in 1976 to 1977 and to 32,000 in 1981. The increase evident from 1973 to 1976-77 may be due, in part, to differences in sieve mesh size used, as finer mesh was used from 1976 onwards (Table 1). Consequently, the sieve losses were less in the latter period but as the same frequency of 2nd, 3rd and 4th instar larvae was found in both periods, the increase can be considered significant.

The colonization of chironomids began near the river inlets, where larval densities in 1968 were between 1,000 and 10,000 ind. m^{-2}. In 1971 and 1973 densities of about 1,000 ind. m^{-2} occurred over extensive areas of the lake, with two localities exhibiting densities above 10,000 ind. m^{-2}. In 1981 larval densities were above 10,000 ind. m^{-2} over most of the lake (Fig. 2).

Most species important in the present chironomid community of Hjarbæk Fjord were already found in 1968, and since then their densities and distributions have increased. Changes for the following species are given in the figures indicated: *Procladius* spp. (Fig. 3), *Chironomus plumosus* f. *semireductus* (Fig. 4), *Cryptochironomus redekei* (Fig. 5), and *Cladotanytarsus* spp. (Fig. 8). The occurrence of *Polypedilum bicrenatum* is more variable; it was not found in 1968, while it was numerous in 1971, and then found sparsely scattered in 1973. In both 1976 to 1977 and 1981 *P. bicrenatum* was one of the major species (Table 3, Fig. 7). A few individuals of *Fleuria lacustris* were first recorded in 1973. In 1976 to 1977, it was abun-

TABLE 3. Average number (nos. m^{-2}) of Oligochaeta and Chironomidae in Hjarbæk Fjord during 1968-81.

	1968	1971	1973	1976-77	1981
Oligochaeta	344	0	1,571	13,835	1,681
Chironomidae					
Procladius sp.	3	109	14	3,824	739
Psectrocladius sp.	0	7	0	310	63
Chironomus plumosus					
f. semireductus	3	57	9	950	1,572
Cryptochironomus redekei	72	264	101	265	567
Fleuria lacustris	0	0	2	2,690	7,871
Glyptotendipes sp.	2	41	5	160	65
Polypedilum bicrenatum	0	2,268	65	3,725	3,431
Polypedilum nubeculosum	0	0	5	410	892
Cladotanytarsus spp.	8	1,328	2,641	6,285	17,126
Tanytarsus spp.	5	6	219	145	65
Other Chironomidae	28	0	0	195	31
Total Chironomidae	121	4,080	3,061	18,959	32,422

Cryptochironomus redekei
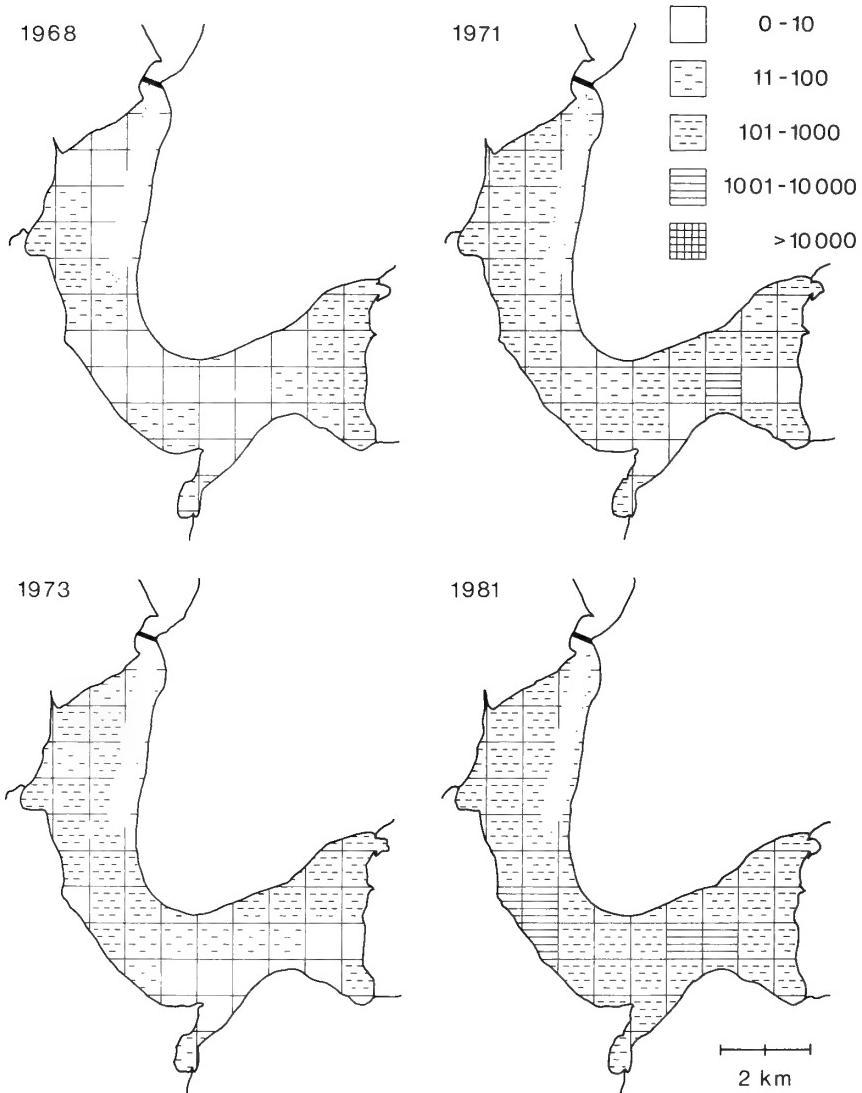
FIG. 5. Distribution of *Cryptochironomus redekei* in Hjarbæk Fjord during 1968-81. Density in nos. m⁻².

dant in the south-eastern part of the lake, and in 1981 it was common throughout the lake, particularly in the southern section, with densities above 10,000 ind. m⁻² (Table 3, Fig. 6).

More than one *Cladotanytarsus* species has been found in Hjarbæk Fjord, and there are indications of alternation amongst these species during the transition of the lake, but due to difficulties in species identification this cannot yet be confirmed.

DISCUSSION

Succession of the chironomid community. — No information on colonization of the chironomids is available for the first two years following the dam construction, when salinity was declining most rapidly. However, the results for 1968 show that the original brackish water community became extinct soon after establishment of the dam, and that the new species settled near the river inlets. These pioneers were mainly freshwater species, but all are known to withstand salinities of at least 5-8 o/oo (Thienemann 1954, Parma and Krebs 1977). Since then, these pioneer species have dominated, and their population size has increased enormously, concomitant with increased primary production. Phytoplankton production reached a maximum in 1974 and has remained at that level since then. In contrast, the chironomid population has continued to increase (Table 3, Fig. 2), while densities of other invertebrates have decreased (Jepsen 1976, Christensen 1979). High pH and ammonium (NH_4^+) concentrations during, at least, the last two summers resulted in fish either being killed or emigrating. Predation on the chironomids was then reduced, which may explain the high larval population in 1981 compared with earlier records (Table 3, Fig. 2).

Fleuria lacustris first appeared in 1973, and, since 1976, has been a dominant member of the community. *F. lacustris* is only known from a few ponds or shallow, brackish or freshwater, lakes in Europe (Lenz 1954-62, Schlee 1980b, Reiss personal comm.) and the USSR (Shilova 1973, Aleksevnina 1974). All habitats of this species are unstable and highly productive systems.

Following salinity decrease of Lake IJsselmeer, the Netherlands, freshwater invertebrates colonized the lake. *Chironomus plumosus* was the dominating chironomid. A diverse invertebrate and fish community became established, and the density of chironomid larvae did not exceed 1,000 to 1,500 ind. m^{-2} (v.d. Toreen 1939, Havinga 1941); this being a much lower density than found in Hjarbæk Fjord.

In newly formed freshwater impoundments, four development stages can be recognized (Morduchai-Boltovskoi 1961, McLachlan 1974): (1) a lentic fauna proliferates in the reservoir's filling period, (2) *Chironomus plumosus* often benefits for a short time, when the original terrestrial organic matter is decomposed, (3) a more diverse fauna with numerous
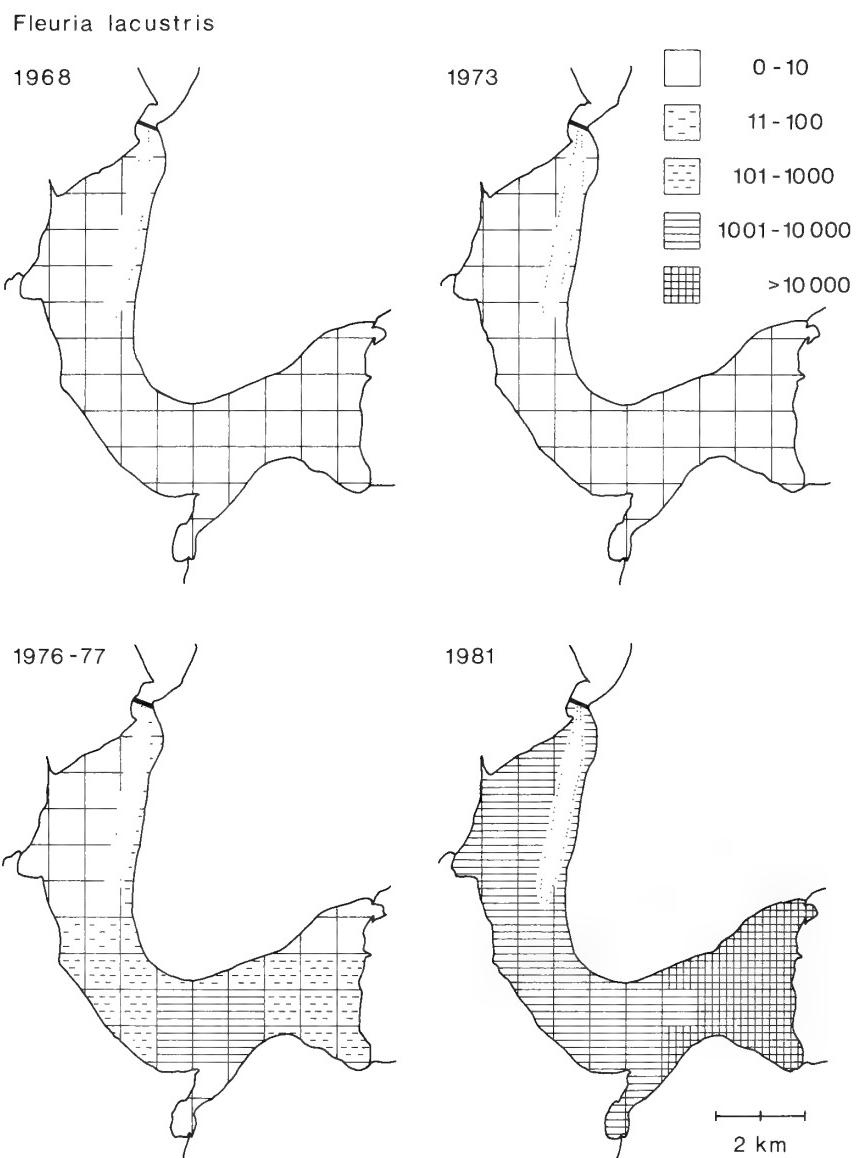
Fleuria lacustris

Fig. 6.   Distribution of *Fleuria lacustris* in Hjarbæk Fjord during 1968-81. Density in nos. m⁻².

Polypedilum bicrenatum
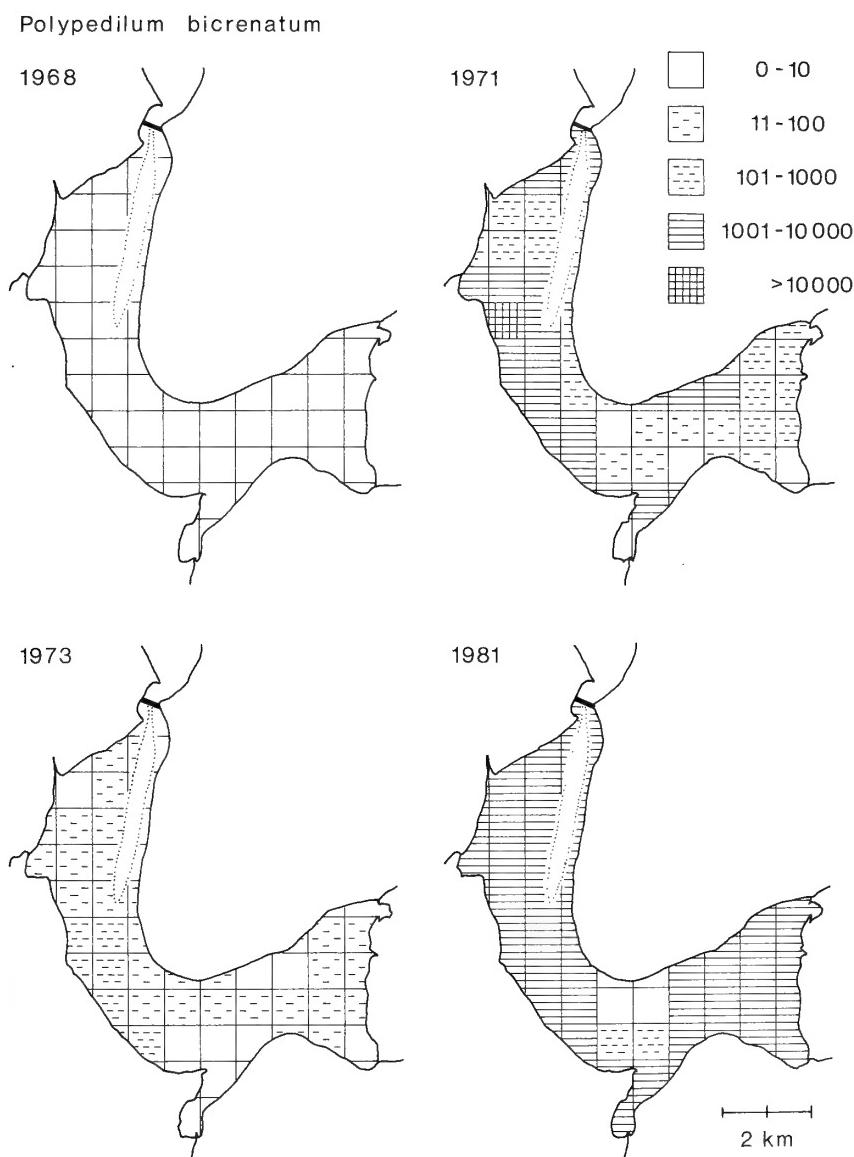
FIG. 7. Distribution of *Polypedilum bicrenatum* in Hjarbæk Fjord during 1968-81. Density in nos. m⁻².

species of oligochaets, chironomids and molluscs appears, which later develops to (4) the final stage where an "equilibrium" of the different species is reached, depending on trophic status and morphometry of the impoundment. The present fauna community in Hjarbæk Fjord, 15 years after the dam construction, has not yet reached an "equilibrium" stage. A diverse invertebrate fauna was found in the lake a few years after the establishment of the dam, but later it was replaced by an oligochaet-chironomid dominated community, whose density is still increasing.

Nuisance problems by midges. — Nuisance problems caused by midges have been reported from a number of sites (see Grodhaus 1975 for references). Outbreaks of chironomids have occurred in brackish water (e.g., the lagoons of the German Baltic Sea Coast, Thienemann 1954), or in brackish water turning into freshwater (e.g., IJsselmeer, Kruseman 1935, v.d. Torren 1939). Recently, Beattie (1981) described an incident of a chironomid plague at Wolderwijd, a border lake to IJsselmeer. There the invertebrate community was assumed to be in "equilibrium", with the chironomid larval density on average 1,000 ind. m^{-2} (mainly *Chironomus plumosus*). Two reasons for such low larval densities causing midge nuisance were stated. Firstly, the mean depth of the lake is 2m, hence most of the 18 km^2 lake bottom is a suitable habitat for chironomid larvae, so the total numbers of adult chironomids emerging from the lake is high. Secondly, the adult midges accumulate at specific localities along the shore, attracted either by light or by swarming points.

In Hjarbæk Fjord, the density of larvae is much higher than in Wolderwijd, and suitable larval habitats are found over 90% of the lake. Prevailing westerly winds concentrate the adult midges in certain areas. The dominating chironomid species have two or three generations per year (Lindegaard and Jónsson, in prep.), and consequently large numbers of adults are present from late May to September.

Two plague types can be recognized at Hjarbæk Fjord: (1) All but one of the chironomid species have normal swarming behavior, forming under suitable weather conditions numerous swarms near the lake. (2) *Fleuria lacustris* shows a very different behaviour (Schlee 1980a,b). Newly hatched adults fly to the shore and cover the substrate in vast masses. A special social contact, in which the individuals touch each other, ensures that the formations do not break up. These formations may be disturbed either by man or by wind, but the midges will immediately try to fly back to reestablish their contacts. At certain times, *F. lacustris* may cover the shore surroundings over large parts of Hjarbæk Fjord. Newly hatched adults may remain for some time at their pupal exuviae, and from there they may

Cladotanytarsus spp.
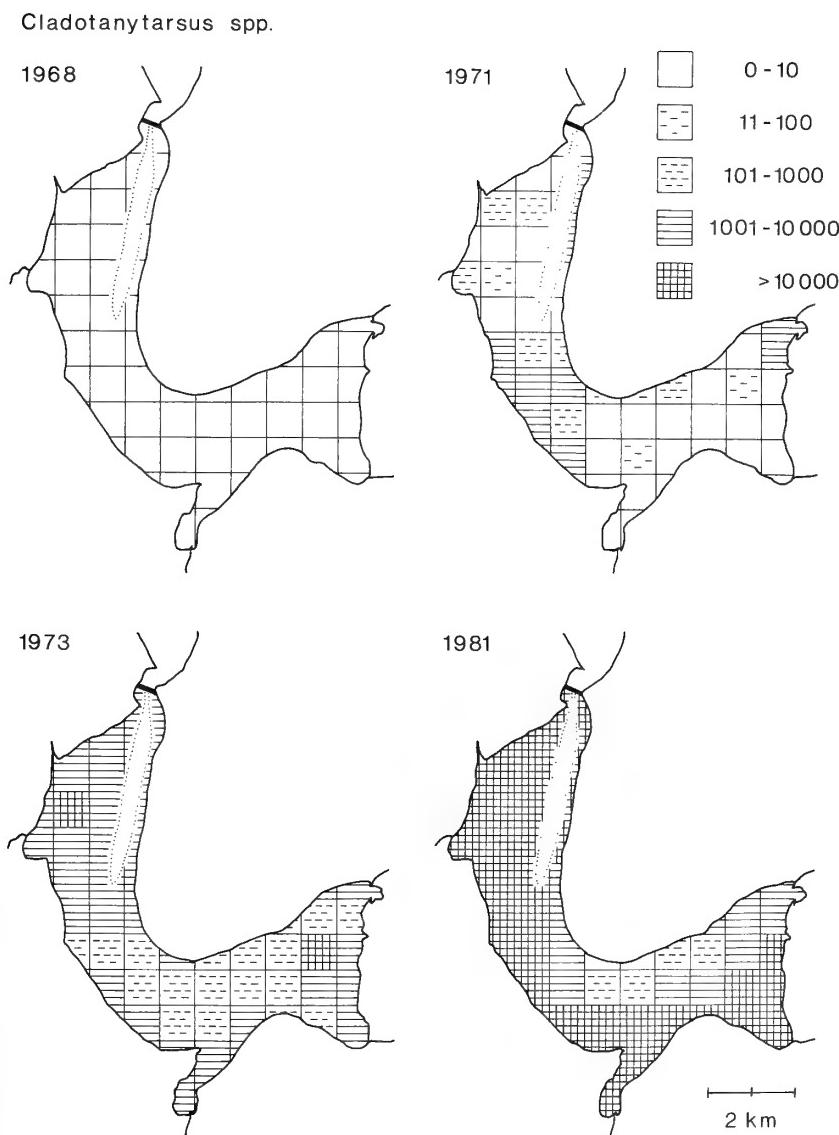
FIG. 8.   Distribution of *Cladotanytarsus* spp. in Hjarbæk Fjord during 1968-81. Density in nos. m^{-2}.

directly invade boats in immense numbers, as they perceive the boats as parts of the shoreline.

We consider several factors contribute to the serious chironomid plague at Hjarbæk Fjord. These are: (1) the average density of 32,000 larvae m^{-2} is higher than normally found in lakes. (2) No severe oxygen depletion occurs in the lake for long periods, and the sandy substrate making up the lake bottom remains undisturbed in stormy weather, thus the larval tubebuilding and food uptake is not disturbed as in shallow mud bottom lakes (Jónasson and Lindegaard 1979). Therefore, more than 90% of the bottom area in Hjarbæk Fjord (i.e., 22 *to* 23 *km²*) is suitable habitat for chironomid larvae. (3) Disappearance of other invertebrates and, to some extent, also of fish populations has resulted in low predation and may have reduced interspecific competition. The emergence of adults is, therefore, relatively high compared to other lakes. (4) Along with normal swarms, the unusual appearance and the special behaviour of *F. lacustris* result in a serious nuisance of crawling midges.

REFERENCES

ALEKSEVNINA, M.S. 1974. Rost i produktsiya massovykh vidov khironomid (Diptera, Tendipedidae) avandel'ty Volgi. (Growth and production of mass species of chironomids (Diptera, Tendipedidae) in the Volga avandelta). Zool. Zh. 53:720-727.

ANDERSEN, F.S. 1949. On the subgenus *Chironomus*. Studies on the systematics and biology of Chironomidae III. Vidensk. Medd. dansk naturh. Foren. 111:1-66.

BEATTIE, D.M. 1981. Investigations into the occurrence of midge plagues in the vicinity of Harderwijk (Netherlands). Hydrobiologia 80:147-159.

CHRISTENSEN, S. 1979. Hjarbæk Fjord 1966-78. Thesis, Freshwater Biological Laboratory, University of Copenhagen.

FITTKAU, E.J. AND F. REISS. 1978. Chironomidae. *In:* Illies, J. (ed.): Limnofauna Europaea, 2nd edition: G. Fischer, Stuttgart, 404-440.

GRODHAUS, G. 1975. Bibliography of chironomid midge nuisance and control. California Vector Veiws 22:71-81.

GRØNTVED, J. 1960. On the productivity of microbenthos and phytoplankton in some Danish fjords. Medd. Danm. Fiskeri- og Havunders. N. S. 3:55-92.

HAVINGA, B. 1941. De veranderingen in den hydrographischen toestand en in de macrofauna von het IJsselmeer gedurende de jaren 1936-1940. Meded. Zuidersee — Comm. ned. dierk. Vereen 5:1-23.

JEPSEN, P.U. 1976. Feeding ecology of Goldeneye (*Bucephala clangula*) during the wing-feather moult in Denmark. Dan. Rev. Game Biol. 10, 4:1-23.

——————. 1978: Vildtreservatet Hjarbæk Fjord (The game reserve Hjarbæk Fjord). Danske Vildtundersøgelser 30:1-68.

JÓNASSON, P.M. AND C. LINDEGAARD. 1979. Zoobenthos and its contribution to the metabolism of shallow lakes. Arch. Hydrobiol. Beih. Ergebn. Limnol. 13:162-180.

KRUSEMAN, G. 1935. 8^a mededeeling over Tendipedidae. Tijdschr. Entomolog. 78: LX-LXII.

LENZ, F. 1933. Untersuchungen zur Limnologie von Strandseen. Verh. Internat. Verein Limnol. 6:166-177.

——————. 1954-62: Die Metamorphose der Tendipedinae (Chironomidae). *In:* Lindner, E. (ed.): Die Fliegen der palaearktischen Region 13c:139-260.

LINDEGAARD, C. AND E. JÓNSSON. (in prep.) Abundance, population dynamics and production of Chironomidae (Diptera) in Hjarbæk Fjord, Denmark, during a period with mass developments.

McLACHLAN, A.J. 1974. The development of chironomid communities in a new temperate impoundment. Ent. Tidskr. 95 suppl.: 162-171.

MORDUCHAI-BOLTOVSKOI, F.D. 1961. Die Entwicklung der Bodenfauna in den Stauseen der Wolga. Verh. Internat. Verein. Limnol. 14:647-651.

MUUS, B.J. 1967. The fauna of Danish estuaries and lagoons. Medd. Danm. Fiskeri- og Havunders., N. S. 5:1-316.

NURSALL, J.R. 1952. The early development of a bottom fauna in a new power reservoir in the Rocky Mountains of Alberta. Can. J. Zool. 30:387-409.

PARMA, S. AND B.P.M. KREBS. 1977. The distribution of chironomid larvae in relation to chloride concentration in a brackish water region of The Netherlands. Hydrobiologia. 52:117-126.

PATERSON, C.G. AND C.H. FERNANDO. 1970. Benthic fauna colonization of a new reservoir with particular reference to the Chironomidae. J. Fish. Res. Bd. Canada. 27:213-232.

SCHLEE, D. 1980a. Ungewöhnliche Varianten des Sozialverhaltens bei Zuckmücken (Diptera: Chironomidae). Stuttgarter Beitr. Naturk. Ser. A 336:1-12.

——————. 1980b. Besonderheiten der Biologie und Morphologie von *Fleuria lacustris* (Diptera: Chironomidae). Stuttgarter Beitr. Naturk. Ser. A 340:1-23.

SHILOVA, A.I. 1973. Novye i maloizvextnye Chironomidae (Diptera) fauny SSR. II. (New and little known Chironomidae (Diptera) of the USSR fauna. II). Inf. Byull. Inst. Biol. vnutr. Vod. 17:48-59.

THIENEMANN, A. 1954. *Chironomus.* Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Die Binnengewässer 20:1-834.

TORREN, G. VAN DER. 1939. Voorlopig verslag van de commissie inzake de muggenplagen om het IJsselmeer. Den Haag, Algemeine Staatsdrukkerij.

Effects of the Squaw Rapids Hydroelectric Development on Saskatchewan River Chironomidae (Diptera)

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ABSTRACT. — Analysis of the Saskatchewan River chironomid fauna in the vicinity of the Squaw Rapids Hydroelectric Development showed that this family represented more than 2/3 of the total number of species of aquatic insects. Comparison of the upstream and downstream fauna showed distinct differences in the chironomid community. Downstream, some upstream species were eliminated and replaced by others, some species became less abundant, others became more abundant and still others remained unchanged. A number of environmental parameters appear to influence the chironomid community. An altered thermal pattern caused delay in the onset of spring emergence of most species examined.

INTRODUCTION

The use of benthic community structure to detect effects of impoundments on riverine ecosystems has been discussed by various authors (Gore, 1980; Fraley, 1979; Williams and Winget, 1979; Brooker and Hemsworth, 1978; Armitage, 1978, 1977; Armitage *et. al.,* 1978; Merkley, 1978; Ward and Short, 1978; Young, *et. al.,* 1976; Goodno, 1975; Olson and Tarter, 1974; Ward, 1976a, 1976b, 1974; Lackey, 1973; Lehmkuhl, 1972; Spence and Hynes, 1971; Hilsenhoff, 1971). Many of these studies, however, have not identified all groups of the community to the species level. The Chironomidae in particular have been neglected, yet they comprise a significant part of the benthic community.

Lehmkuhl (unpublished) studied the benthos of the Saskatchewan River in the vicinity of the Squaw Rapids hydroelectric development. He found approximately 62 species of aquatic insects, excluding the Chironomidae (Table I). The study reported herein of the Chironomidae in this part of the river was undertaken to complement Lehmkuhl's information.

The objectives were to (1) discover which species of chironomids occur upstream, within and downstream of the hydroelectric development and (2) define the effect of the development on the chironomid community.

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TABLE 1.   Insects other than Chironomidae known to occur in the Saskatchewan River associated with Tobin Lake.

Ephemeroptera
    Ametropodidae
        Ametropus albrighti Traver
    Baetidae
        Baetis tricaudatus Dodds
        Baetis sp. 2
        Baetis sp. 3
        Centroptilum bifurcatum McDunnough
        Centroptilum rivulare Traver
        Pseudocloeon sp. 1
        Pseudocloeon sp. 2
    Caenidae
        Brachycersus prudens (McDunnough)
        Caenis tardata McDunnough
    Ephemerellidae
        Ephemerella inermis Eaton
    Ephemeridae
        Ephoron album Say
    Heptageniidae
        Anepeorus rusticus (McDunnough)
        Heptagenia elegentula Eaton
        Heptagenia flavescens (Walsh)
        Heptagenia pulla Clemens
        Heptagenia solitaria McDunnough
        Macdunnoa nipawinia Lehmkuhl
        Pseudiron centralis McDunnough
        Rhithrgena jejuna Eaton
        Stenacron interpunctatum (Say)
        Stenonema terminatum Walsh

    Leptophlebiidae
        Leptophlebia cupida (Say)
        Traverella albertana (McDunnough)
    Metretopodidae
        Metretopus borealis Eaton
        Siphloplecton interlineatum (Walsh)
    Oligoneuriidae
        Lachlania saskatchewanensis Ide
    Tricorythidae
        Tricorythodes corpulentus Kilgore and Allen
        Tricorythodes minutus Traver

Plecoptera
    Chloroperlidae
        Hastaperla brevis (Banks)

TABLE 1.   (cont'd)

Perlidae
  Acroneuria abnormis (Newman)
Perlodidae
  Isogenoides colubrinus (Hagen)
  Isoperla bilineata (Say)
  Isoperla longiseta Banks
Pteronarcidae
  Pteronarcys dorsata (Say)

Odonata
 Gomphidae
  Gomphus intricatus Hagen
  Gomphus notatus Bambur
  Ophiogomphus severus Hagen

Hemiptera
 Corixidae

Trichoptera
 Brachycentridae
  Brachycentrus occidentalis Banks
 Glossosomatidae
  Protoptila tenebrosa (Walker)
 Hydropsychidae
  Cheumatopsyche spp.
  Hydropsyche gutatta Pictet
  Hydropsyche occidentalis Banks
  Hydropsyche placoda Ross
  Hydropsyche recurvata Banks
 Hydroptilidae
  Hydroptila sp.
  Mayatrichia ayama Mosely
 Leptoceridae
  Athripsodes arielles Denning
  Ceraclyia sp.
  Nectopsyche diarina (Ross)
 Polycentropidae
  Neureclipsis bimaculata (Linnaeus)
 Psychomyiidae
  Psychomyia flavida Hagen

Coleoptera
 Dytiscidae

Diptera
 Simuliidae
  Simulium arcticum Malloch
  Simulium luggeri Nicholson and Mickel

TABLE 1.   (cont'd)

Simulium meridionale Riley
Simulium rugglesi Nicholson and Mickel
Simulium venustum Say
Tabanidae
Tipulidae

STUDY AREA

The Saskatchewan River system originates in the Rocky Mountains in western Canada. The upper reaches consists of two branches, the North and South Saskatchewan Rivers which flow more than 1200 kilometers eastward before converging to form the main Saskatchewan River which flows east for another 544 kilometers to Lake Winnipeg. The study focused on the Saskatchewan River in the vicinity of Tobin Lake (Figure 1), a hydroelectric development reservoir in central eastern Saskatchewan (N. lat. 53 30'; W. long. 103 30').

The lake, completed in 1962, is 74 kilometers long and covers an area of 30,000 hectares. The maximum water depth of 25.5 meters occurs at the dam. Water is taken from the lake through conduits submerged 4.8 meters below the surface, leading to the power canal. The water travels 4.8 kilometers in the power canal to the generating station where it passes through turbines and back into the Saskatchewan River.

METHODS

Five sampling stations, located about 85 kilometers upstream from the dam, within the impoundment and 6 and 23 kilometers downstream from the dam were chosen (Fig. 1). Collections of chironomids were made at each station during 1979, 1980 and 1981 to discover the species in the system. The pupal exuvial method was used during 1980 and 1981 to characterize community composition and emergence patterns in the River (Rossaro and Ferrarese, 1980; Laville, 1979; Wilson, 1979, 1977; Rossaro, 1978; Wilson and McGill, 1977; Wartinbee, 1976; Coffman, 1973; Wilson and Bright, 1973; and Brundin, 1966). Samples were taken from June to August in 1980 and April to November in 1981. Specimens were obtained in a plankton net with a mesh size of 80 μm, in two ways: (1) the net was held in flowing water for 10 minutes with ½ of the diameter below the surface and; (2) the net was held in a similar manner but dragged for 10 meters. Each sample was emptied into a pint jar of 95% ethanol and taken to the laboratory for analysis. Temperature, oxygen and current velocity were measured following each collection at each site.
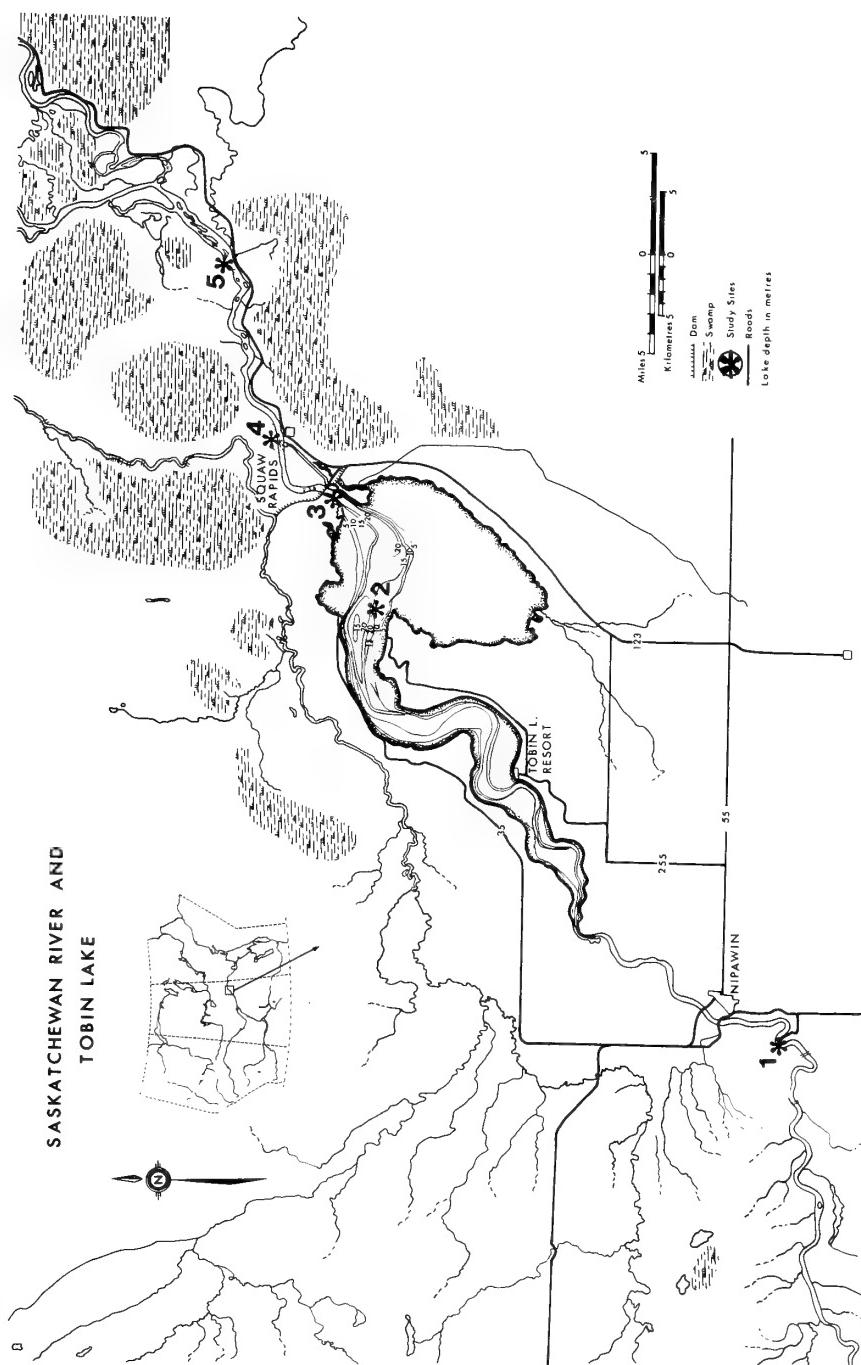
FIG. 1. Saskatchewan River and Tobin Lake.

Samples were sorted in the laboratory, the number of each species counted and representatives placed on microscope slides for identification. Large samples were subsampled using the method described by Wartinbee (1979).

Environmental data for each site was obtained from Saskatchewan Environment for the period (1979-1981). Additional information was taken from Durban (1981), Sawchyn (1974) and Royer (1969). Based on these data, and the surface temperature, oxygen and current velocity measurements taken during the study, a matrix was derived for principle components analysis (PCA) to determine differences between sampling sites and the parameters responsible for these differences. The PCA was done using the SPSS statistical package program (Nie *et. al.*, 1975).
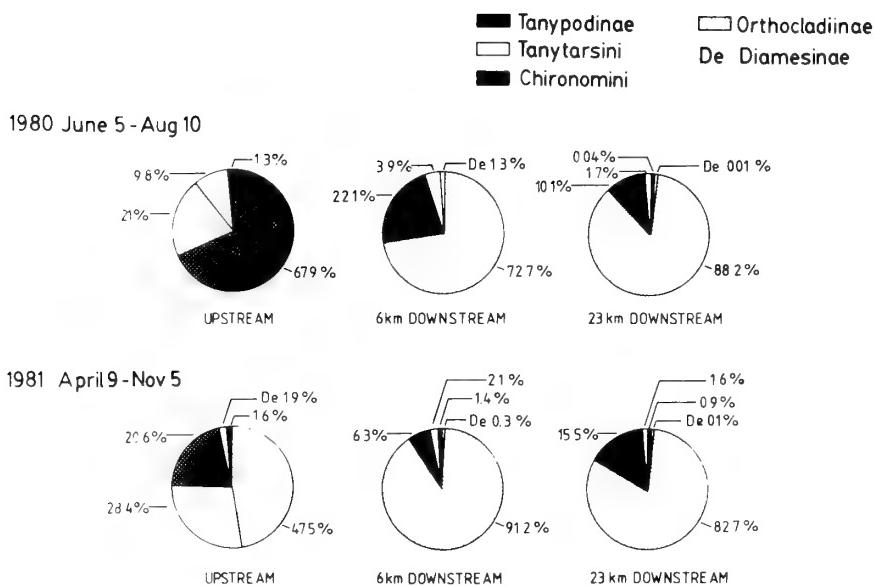
FIG. 2. Composition of the chironomid population at each station during 1980 and 1981 (total number for each site is approximately 30,000).

RESULTS AND DISCUSSION

Chironomid Community — One hundred and thirty-one chironomid species (Table II) were collected from the Saskatchewan River and Tobin Lake. Nine of these occurred only in the lake and are typical lentic species (Table III). Thus, 122 species of chironomids were collected from the Saskatchewan River proper. Based on the species of aquatic insects collected from the study area, the Chironomidae constitute more than 2/3 of the fauna.

Figure 2 shows the relative sizes of the populations of each major chironomid group for the entire period collected during 1980 and 1981. The difference in abundance of the groups, particularly the Chironomini, between years is due to the shorter sampling period in 1980 (June 5 to August 9) compared to that in 1981 (April 9 to November 5, the entire ice-free period). The Orthocladiinae tended to dominate in the early and late parts of the field season in 1981, while the Chironomini dominated during the middle period. As it is thus important to take samples during the entire ice-free season only the 1981 data will be discussed in detail.

The fauna in the Saskatchewan River changes from a Chironominae-Orthocladiinae community upstream to one dominated by the Orthocladiinae downstream (Fig. 2). The number of individuals of Tanytarsini is reduced downstream but at the same time there are more species downstream (Table IV). The number of individuals and species of Chironomini are fewer downstream compared to upstream while the Orthocladiinae are rather constant in number of species at both locations (Table IV).

Examination of weekly community structure gives additional information on the changes occurring. There is a clear delay of about 2 weeks in the onset of spring emergence downstream (Fig. 3), with 13 species emerging in the 2nd week of May upstream but only 2 downstream. However, from the beginning of June until the end of the field season the numbers of species emerging at upstream and downstream sites show no apparent difference. Depending on the week selected there may be more species emerging upstream from the reservoir than 23 kilometers downstream and vice versa.

The number of species of major groups during the course of the 1981 field season is shown in Figures 4-6. Upstream, emerging Orthocladiinae dominate during the cooler parts of the field season (April, May, September, October and November) while emerging Chironominae are most abundant during the warmer months. Downstream, however, the Orthocladiinae dominate throughout the season. The Chironomini are abundant during the summer but are not as abundant as at the upstream site.

TABLE 2.   Chironomidae in Tobin Lake and adjacent stretches of the Saskatchewan River.

Tanypodinae
      Pentaneurini
            Ablabesmyia (s.s.) sp. 1
            Ablabesmyia (s.s.) sp. 2
            Ablabesmyia (s.s.) sp. 3
            Conchapelopia (s.s.) *telema* Roback
            Rheopelopia sp.
            Thienemannimyia senata (Walley)
      Procladiini
            Procladius (s.s.) *denticulatus* Sublette
            Procladius (s.s.) *freemani* Sublette
            Procladius (Psilotanypus) bellus (Loew)

Diamesinae
      Diamesini
            Diamesa cf. *cinerella* Meigen
            Potthastia longimana Kieffer

Chironominae
      Chironomini
            Chernovskiia amphitrite (Townes)
            Chironomus (s.s.) *anthracinus* Zetterstedt
            Chironomus (s.s.) *decorus* Johannsen
            Chironomus (s.s.) *plumosus* (Linnaeus)
            Chironomus (s.s.) sp. 1
            Chironomus (s.s.) sp. 2
            Chironomus (s.s.) sp. 3
            Cladopelma sp.
            Cryptochironomus digitatus Malloch
            Cryptochironomus scimitarus (Townes)
            Cryptochironomus stylifera Johannsen
            Cryptochironomus sp. 1
            Cryptochironomus sp. 2
            Cryptochironomus sp. 3
            Cryptochironomus sp. 4
            Cryptotendipes darbyi Sublette
            Cyphomella gibbera Saether
            Demicryptochironomus sp.
            Dicrotendipes nervosus Staeger
            Endochironomus nigricans Johannsen
            Glyptotendipes (Phytotendipes) lobiferus (Say)
            Glyptotendipes (Phytotendipes) paripes (Edwards)

            Harnischia curtilamellata (Malloch)
            Microtendipes caducus Townes
            Microtendipes pedellus (De Geer)
            Nilothauma babiyi (Rempel)
            Parachironomus abortivus (Malloch)

TABLE 2.   (cont'd)

Parachironomus frequens (Johannsen)
Paracladopelma nereis (Townes)
Paracladopelma winnelli Jackson
Paracladopelma sp. 1
Paracladopelma sp. 2
Paracladopelma sp. 3
Paralauterborniella nigrohalterale (Malloch)
Paratendipes albimanus (Meigen)
Phaenopsectra obediens (Johannsen)
Polypedilum (s.s.) sp. nr. *aviceps* Townes
Polypedilum (s.s.) *convictum* (Walker)
Polypedilum (s.s.) *fallax* (Johannsen)
Polypedilum (s.s.) *illinoense* (Malloch)
Polypedilum (s.s.) *laetum* (Meigen)
Polypedilum (s.s.) *obtusum* Townes
Polypedilum (Tripodura) digitifer Townes
Polypedilum (Tripodura) scalaenum (Schrank)
Polypedilum (Tripodura) sp. 1
Polypedilum (Tripodura) sp. 2
Polypedilum (Tripodura) sp. 3
Robackia claviger (Townes)
Robackia demeijerei (Kruseman)
Saetheria tylus Jackson
Stenochironomus hilaris (Walker)
Stictochironomus sp. 1
Stictochironomus sp. 2
Stictochironomus sp. 3
Xenochironomus (Anceus) scopula Townes
Chironomini Genus 1 sp.
Chironomini Genus 2 sp.

Tanytarsini
Cladotanytarsus sp. nr. viridiventris (Malloch)
Cladotanytarsus sp.
Constempellina sp.
Micropsectra nigripila (Johannsen)
Micropsectra dives (Johannsen)
Micropsectra polita (Malloch)
Micropsectra sp.
Paratanytarsus confusus Palmen
Paratanytarsus sp. nr. *dimorphis* Reiss
Paratanytarsus laccophilus (Edwards)
Paratanytarsus sp. nr. *natvigi* (Goetghebuer)
Paratanytarsus sp. 1
Paratanytarsus sp. 2
Rheotanytarsus exiguus (Johannsen)
Rheotanytarsus sp. 1
Rheotanytarsus sp. 2

TABLE 2. (cont'd)

Stempellinella sp.
Tanytarsus glabrescens Edwards
Tanytarsus guerlus Roback
Tanytarsus sp. 1
Tanytarsus sp. 2
Tanytarsus sp. 3
Chironominae Genus 3 sp.

Orthocladiinae

Acricotopus sp.
Cardiocladius sp.
Cricotopus (s.s.) *bicintus* (Meigen)
Cricotopus (s.s.) *curtus* Hirvenoja
Cricotopus (s.s.) *politus* (Coquillett)
Cricotopus (s.s.) *slossonae* Malloch
Cricotopus (s.s.) *triannulatus* (Macquart)
Cricotopus (s.s.) cf. *tremulus* (Linnaeus)
Cricotopus (s.s.) sp. 1 nr. *tremulus* (Linnaeus)
Cricotopus (s.s.) sp. 2 nr. *tremulus* (Linnaeus)
Cricotopus (s.s.) *trifascia* Edwards
Cricotopus (s.s.) sp.
Cricotopus (Isocladius) intersectus (Staeger)
Cricotopus (Isocladius) sylvestris (Fabricius)
Eukiefferiella sp.
Nanocladius (s.s.) *anderseni* Saether
Nanocladius (s.s.) *crassicornis* Saether
Nanocladius (s.s.) *spiniplenus* Saether
Orthocladius (Euorthocladius) rivicola Kieffer
Orthocladius (Euorthocladius) ?rivicola Kieffer
Orthocladius (s.s.) *carlatus* (Roback)
Orthocladius (s.s.) *mallochi* Kieffer
Orthocladius (s.s.) *nigritus* Malloch
Orthocladius (s.s.) *obumbratus* Johannsen
Orthocladius (s.s.) *robacki* Soponis
Orthocladius (s.s.) sp.
Parakiefferiella (s.s.) *torulata* Saether
Psectrocladius (Allopsectrocladius) flavus Johannsen
Psectrocladius (s.s.) *simulans* (Johannsen)
Psectrocladius (s.s.) sp. 1
Psectrocladius (s.s.) sp. 2
Psectrocladius ss. sp. 3
Pseudosmittia sp.
Rheosmittia sp. 1
Rheosmittia sp. 2
Synorthocladius semivirens (Kieffer)
Thienemanniella cf. *xena* Roback
Tvetenia vitracies (Saether)
Orthocladiinae Genus 1 sp.
Orthocladiinae Genus 2 sp.
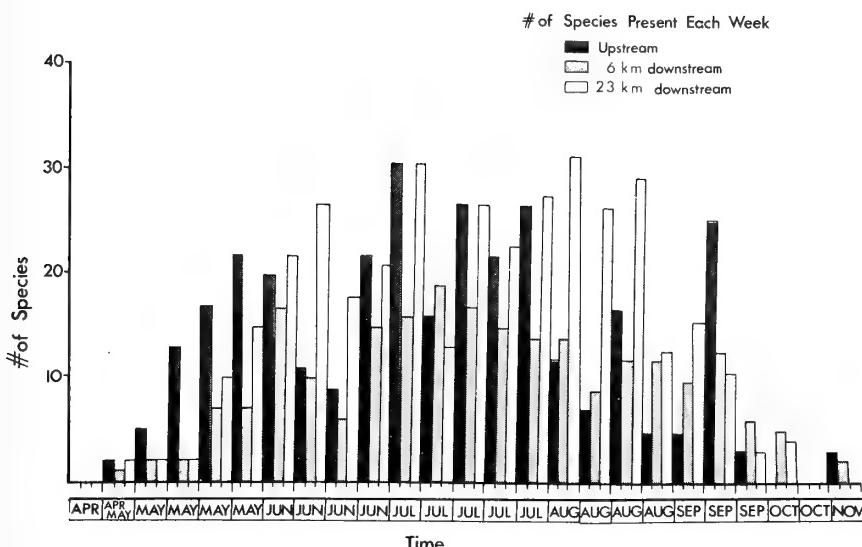
Fig. 3.   Total number of chironomid species collected each week from Saskatchewan River upstream, 6 kilometers downstream and 23 kilometers downstream from Squaw Rapids Dam.

This reinforces the earlier observation that it is necessary to sample during the entire ice-free season to obtain a true picture of the river fauna.

The thirty most abundant species were examined in detail and the following observations were made. While the upstream species *Cyphomella gibbera* and *Stenochironomus hilaris* appear to be eliminated downstream from the reservoir, another, *Polypedilum obtusum,* which is not present upstream, appears in the community. *Rheotanytarsus exiguus* and *Nanocladius anderseni,* the dominant species upstream, show reduced numbers downstream, *Cricotopus bicinctus, Orthocladius carlatus* and *Synorthocladius semivirens,* a small part of the upstream fauna, increase in abundance in the downstream community. *Orthocladius rivicola* and *Tvetenia vitracies* constitute about the same percent of the populations upstream and downstream.

The Orthocladiinae species, *Synorthocladius semivirens* and *Cricotopus* spp. are most abundant during midsummer downstream from the Dam while the numerous Chironomini species are most important above the reservoir. It appears as though some Orthocladiinae species replaced Chironomini species as the most abundant group during the summer. Mackey (1977b) noted that *Cricotopus bicinctus* and *Cricotopus sylvestris* dominated the summer fauna in the Thames River and the River Kent in Britain.

TABLE 3.   Species of Chironomidae found only in Tobin Lake.

Chironomus (s.s.) *anthracinus* Zetterstedt
Chironomus (s.s.) *plumosus* (Linnaeus)
Cladopelma sp.
Cryptochironomus stylifera Johannsen
Cryptochironomus sp. 1
Cryptochironomus sp. 4
Paratanytarsus sp. 1
Psectrocladius (s.s.) sp. 2
Ablabesmyia (s.s.) sp. 3
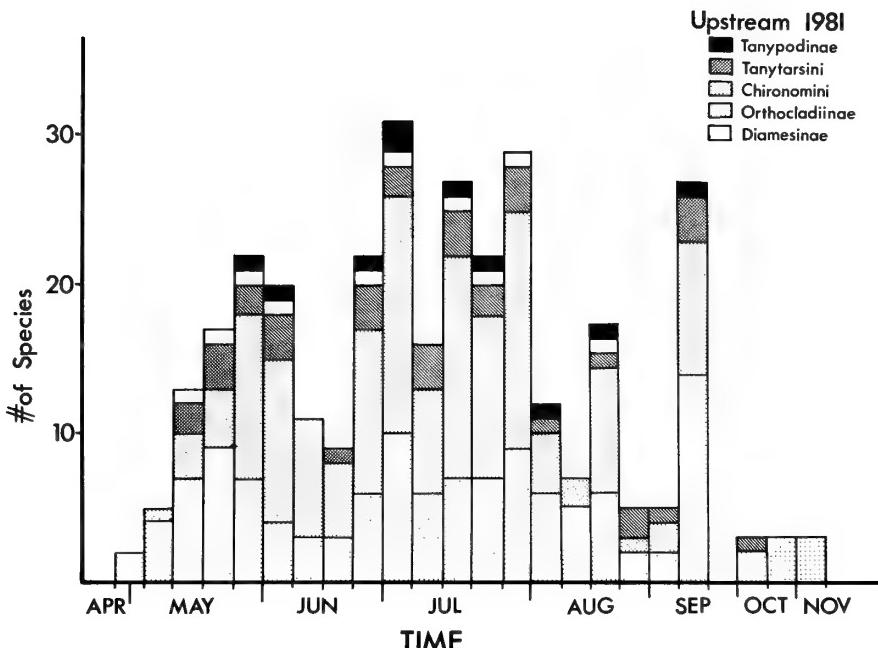
FIG. 4.   Number of species of each major chironomid group collected weekly upstream from Squaw Rapids Dam.

Environmental Factors — In addition to the information presented, studies by Lehmkuhl (1972), Brooker and Hemsworth (1979), Fraley (1979), Williams and Winget (1979), Merkely (1978), Ward (1976a, 1976b), Young *et. al.* (1976), Ward (1974), and Hilsenhoff (1971) have shown altered downstream community structure, presumably because of downstream environmental changes resulting from the presence of reservoirs.

Ward and Stanford (1979) state that temperature, flow and substrate are the major factors affecting macroinvertebrate distribution below reservoirs.

TABLE 4. Number of species of each major group of the Chironomidae at upstream and downstream sites on the Saskatchewan River.

	upstream	½ mile downstream	11 miles downstream
Chironomini	39	20	34
Tanytarsini	9	10	17
Orthocladiinae	25	22	28
Tanypodinae	5	3	3
Diamensinae	1	1	2
TOTALS	79	56	84
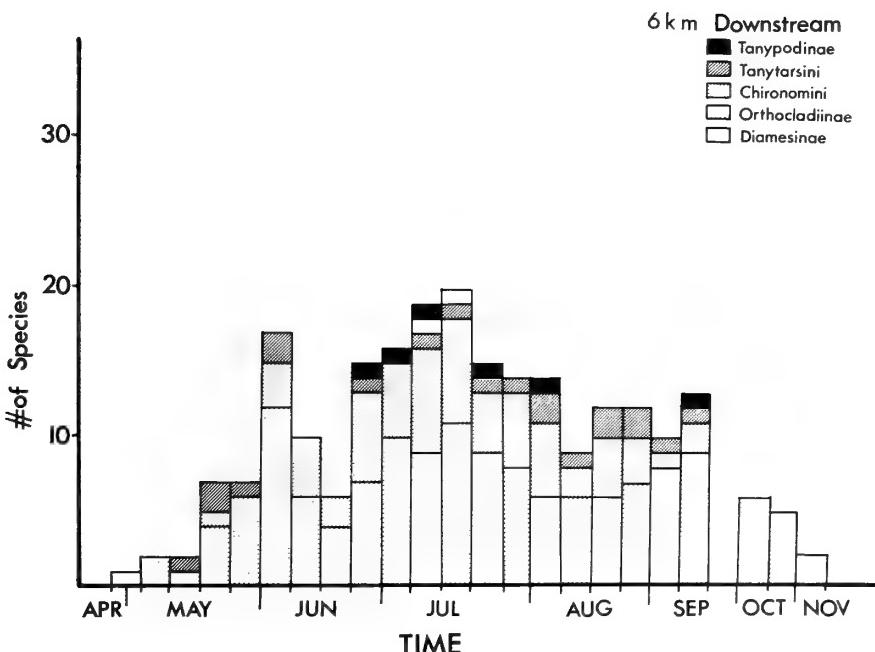
FIG. 5. Number of species of each major chironomid group collected weekly 6 kilometers downstream from Squaw Rapids Dam.

Lehmkuhl (1979) concluded that temperature was the single most important environmental parameter affecting the fauna downstream from a reservoir.

In an attempt to discover how the environment influences the community, environmental parameters were measured at the study sites and comparison made.
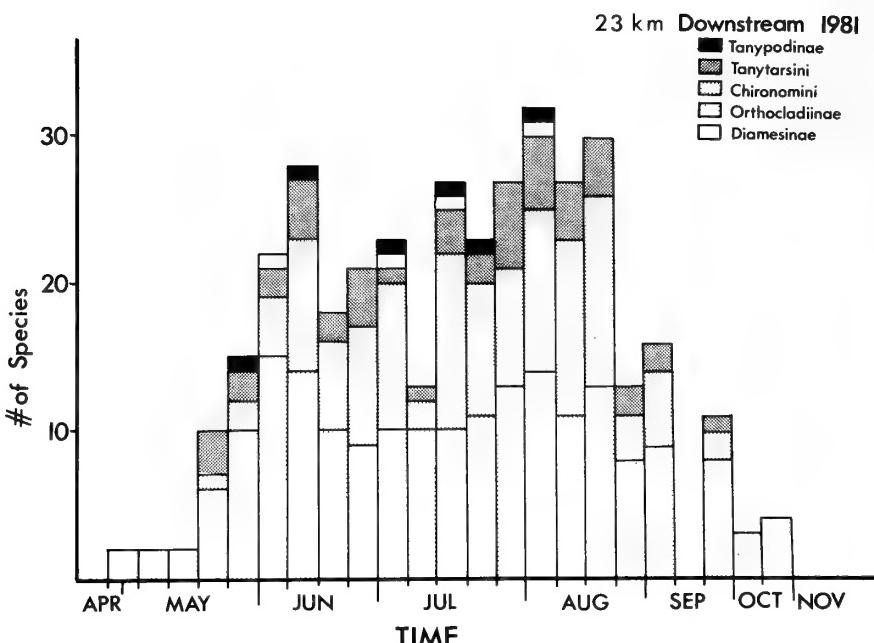
FIG. 6.   Number of species of each major chironomid group collected weekly 23 kilometers downstream from Squaw Rapids Dam.

(i)   *PCA analysis of seasonal averages.*—Average seasonal values of 27 environmental parameters, for example oxygen, temperature, substrate organic carbon, turbidity and months of ice cover, were used in a Principal Components Analysis of the sample sites. Figure 7 is a plot of the principal factor scores of the five sites (2 lake, 3 river) studied. Those scores furthest from the origin, in either direction, on a given axis account for more of the variation (differ from the others more) than those scores closest to the origin. The horizontal Axis (1) accounts for 49.5% of the variation and separates the upstream site from the downstream sites. The lake sites are separated from the river sites on the vertical Axis (2) which accounts for 43.9% of the variation. Thus, the three major categories of sites differ from one another. The scattergram of the environmental parameters (Figure 8) shows high factor loadings for most of the parameters suggesting that all are important in separating sites.

Based on average seasonal values, PCA analysis shows that upstream, lake and downstream sites differ from each other but that no single environmental parameter stands above the others. Therefore, we turned to data from weekly measurements.

Factor 2

Principle Factor Scores for Sites based on
27 Environmental Parameters

Horizontal Factor 1 49.5% of Variation
Vertical Factor 2 43.9% of Variation

① Sask River Upstream
② Tobin Lake at Corral
③ Tobin Lake at Dam
④ Sask River 6 km Downstream
⑤ Sask River 23 km Downstream

②③

Factor 1

④
⑤

①
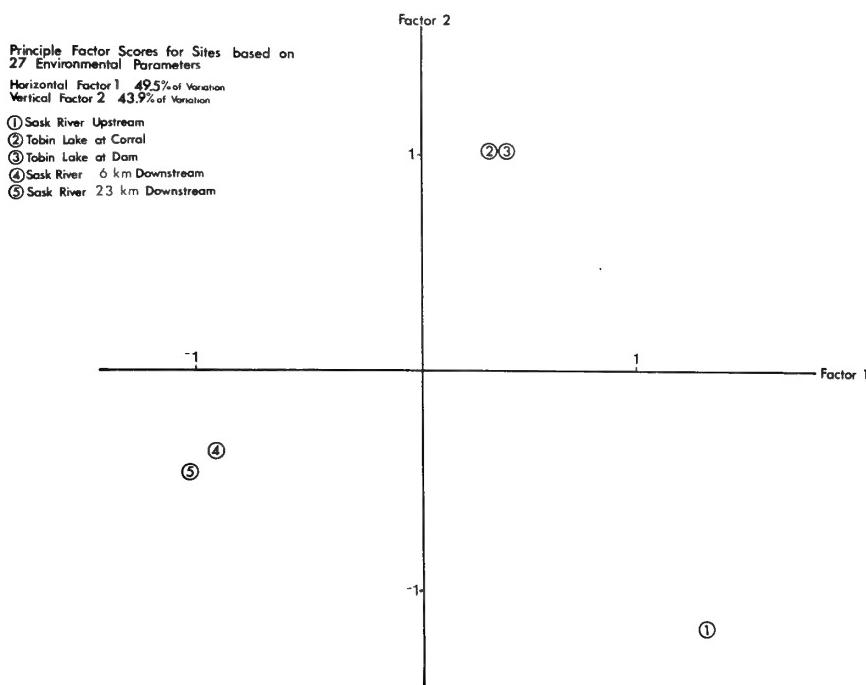
FIG. 7.   Principle factor scores for sites based on 27 environmental parameters (Factors 1 and 2).

(ii) *Data from weekly measurements.*—Our data showed that environmental parameters such as current velocity, substrate and organic carbon have some limited influence on the distribution of individual species in the chironomid community and a detailed discussion is beyond the scope of this paper. Details are discussed in another paper (Mason and Lehmkuhl, in prep'n).

Danks (1978) concluded that temperature and photoperiod are the two most important environmental factors affecting emergence time. In our analysis emergence patterns for each site are compared for the same time, and thus photoperiod is the same, and cannot account for observed differences. Nordlie and Arthur (1981) noted from the literature that oxygen also affects emergence. In our study, oxygen was always at or near saturation, and therefore it probably had little or no effect on chironomid emergence. Thus, the effect of temperature remains and will be examined especially as it relates to chironomid emergence.

Factor 2

•24

•9

•7

•13
18 •25
•8

•27

•17
•16

•10

•4,23
•19

•21

•12 ———— Factor 1

•26

•5

•1

•11

•15

PCA Scattergram of
Environmental Parameters
Horizontal Factor 1   49.5% of Variation
Vertical Factor 2   43.9% of Variation

•20

1·CURRVAR	2·DEGDAY
3·OXYGEN	4·TOTPO4
5·TOTC	6·INORGC
7·ORGC	8·TOTN
9·DISNO2	10·TOTNH3
11·BOD	12·SPECCON
13·DISCL	14·TOTALK
15·PH	16·TDS
17·CA	18·MG
19·NA	20·K
21·SO4	22·TURB
23·MONICEC	24·SUB1
25·SUB2	26·SUB3
27·SUB4	

•3

•2 •14

•22

FIG. 8.   PCA scattergram of environmental parameters (Factors 1 and 2).

It is clear that reservoirs modify the temperature regime of a river depending on release depth and thermal stratification (Ward and Stanford, 1979). Tobin Lake is an epilimnion release reservoir and the downstream thermal pattern is modified directly by lake surface temperatures. Temperature (Fig. 9) showed very definite seasonal differences between the upstream and downstream sites. This pattern was also observed in 1974, 1979 and 1980 and can be considered typical of the system.

Observation of the emergence patterns of eight representative species (Figs. 10-17) showed that a definite delay in the onset of spring emergence occurred downstream. *Microtendipes caducus* and *Orthocladius rivicola* are the only two of these species which appear at the upstream and downstream sites simultaneously. *M. caducus,* however, is more abundant initially upstream than it is downstream. *Polypedilum laetum, Robackia demeijerei, Rheotanytarsus exiguus, Potthastia longimana, Cricotopus trifascia* and
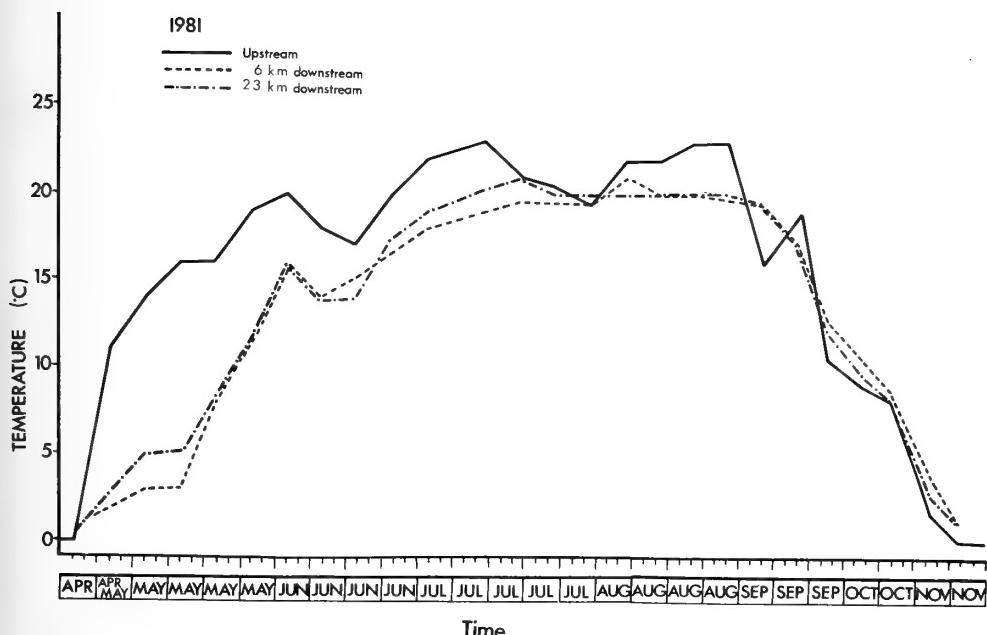
Fig. 9.   Temperature (degrees centigrade) in the Saskatchewan River during the 1981 Field Season.

Tventenia vitracies all appear downstream almost a month after they do upstream. This appears to be the situation for many other species as well. Lesage and Harrison (1980) concluded that the rising spring water temperatures induced the spring emergence of *Cricotopus* spp.

Most studies involving the effects of temperature on chironomid emergence have considered elevated temperatures only. Kochn and Frank (1979), Ferguson and Fox (1978), Langeford (1975) and Langeford and Duffern (1975) concluded that increased water temperatures had no effect on the emergence of aquatic insects. However, Nordlie and Arthur (1981) state that Brittain (1976) and Newel and Minshall (1978) concluded that alteration of normal thermal cycles can cause different developmental rates in aquatic insect life cycles and therefore produce variations in emergence times.

Lesage and Harrison (1980) determined that emergence of *Cricotopus trifascia* occurred between 16 and 21 degrees Celsius, *C. sylvestris* emerged at 18-19 degrees Celsius, and *C. slossonae* and *C. politus* emerged when the water was 20-21 or 22-23 degrees Celsius. A delay in reaching the threshold ambient temperature would therefore result in delay in the onset of
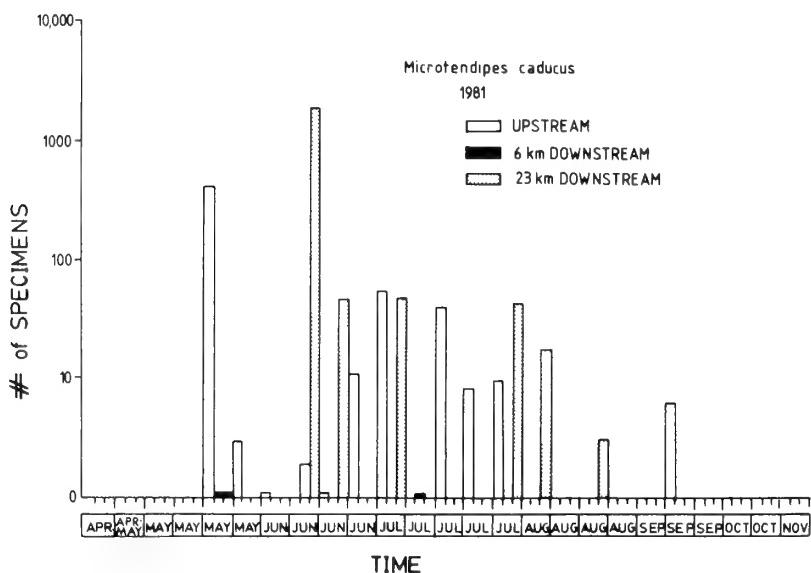
FIG. 10.   Emergence of *Microtendipes caducus* in the Saskatchewan River during 1981.
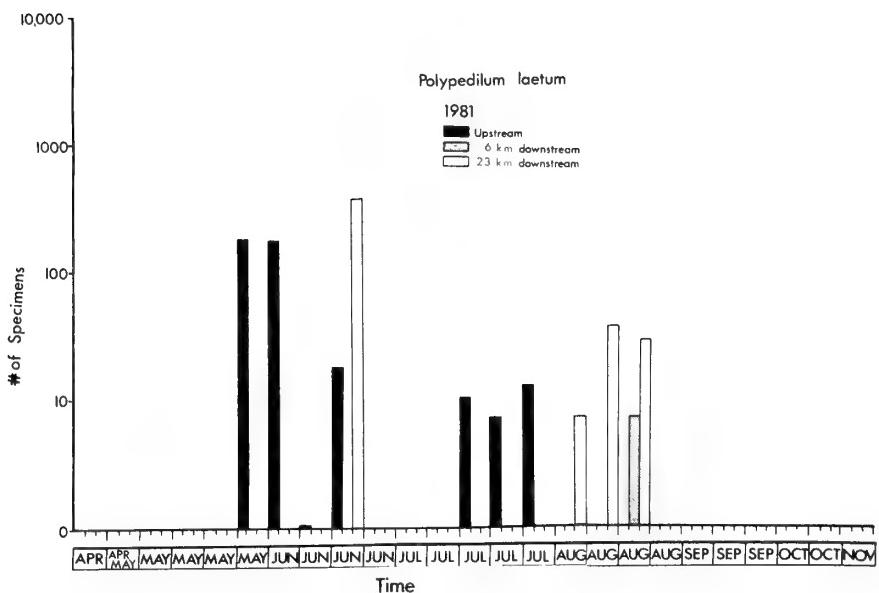
FIG. 11.   Emergence of *Polypedilum laetum* in the Saskatchewan River during 1981.
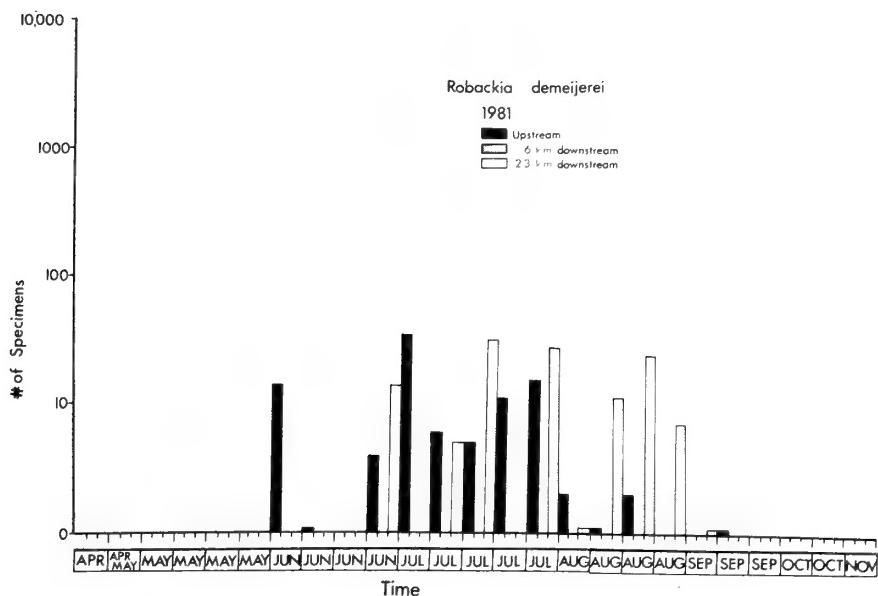
FIG. 12. Emergence of *Robackia demeijerei* in the Saskatchewan River during 1981.
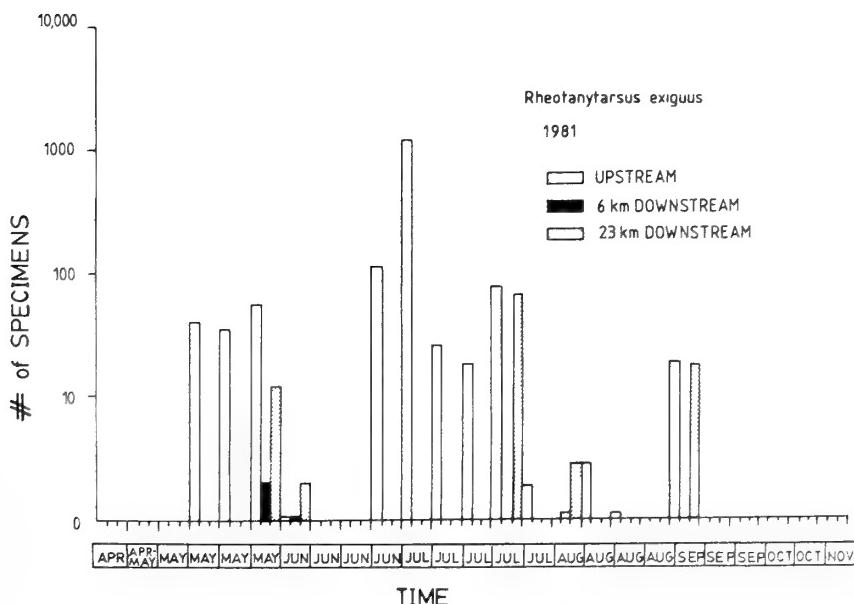
FIG. 13. Emergence of *Rheotanytarsus exiguus* in the Saskatchewan River during 1981.
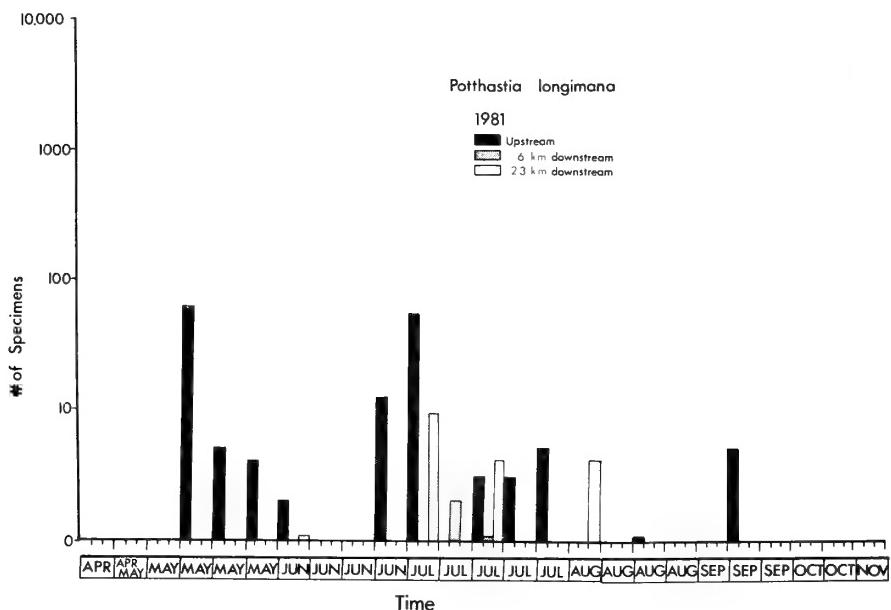
FIG. 14.   Emergence of *Potthastia longimana* in the Saskatchewan River during 1981.
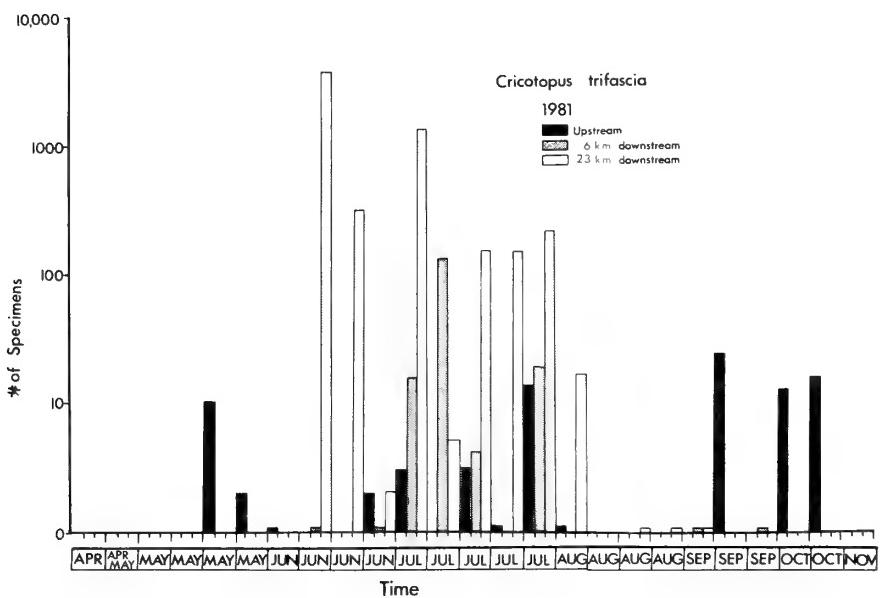
FIG. 15.   Emergence of *Cricotopus trifascia* in the Saskatchewan River during 1981.
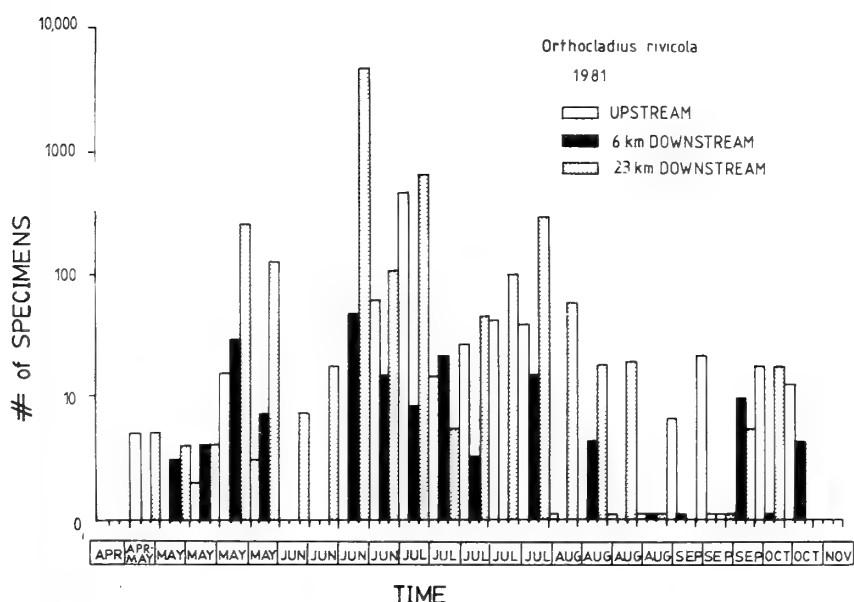
FIG. 16. Emergence of *Orthocladius rivicola* in the Saskatchewan River during 1981.

emergence of a species. This appears to be the situation in the Saskatchewan River in the vicinity of the Squaw Rapids hydroelectric development.

Chironomids made up more than 2/3 of the known aquatic insect species in a regulated portion of the Saskatchewan River. Comparison of the chironomid fauna upstream and downstream from the Squaw Rapids hydroelectric develoment showed distinct differences — some species were eliminated downstream — others decreased in relative abundance, others increased in relative abundance and — still others were apparently not greatly affected by the reservoir. A delayed rise in spring temperature, while not apparently restricting chironomid distribution, caused delays of up to one month in the onset of spring emergence of most species examined. Other environmental parameters, particularly current velocity, substrate and organic carbon appear to affect distribution and growth and review of the available data is being done to determine the precise nature of their influence on the chironomid fauna.
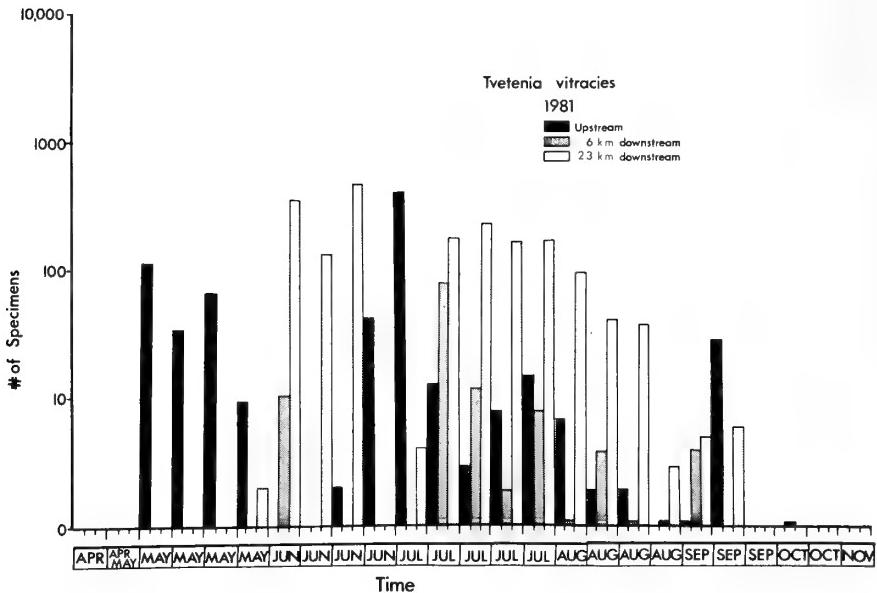
FIG. 17.   Emergence of *Tvetenia vitracies* in the Saskatchewan River during 1981.

REFERENCES

ARMITAGE, P. D.   1977.   Invertebrate drift in the regulated river Tees and an unregulated tributary Maize Bec. below Cow Green dam. Freshwat. Biol. 7:167-183.
—————.   1978.   The impact of Cow Green Resevoir on invertebrate populations in the River Tees. Fresh. Biol. Assoc. Ann. Report 46:47-57.
ARMITAGE, B.J., T.D. FORSYTHE, E.B. RODGERS AND W.B. WRENN.   1978.   Brown Ferry biothermal research series I. Colonization by periphyton, zooplankton and macroinvertebrates. U.S. Env. Pro. Ag. Report #EPA-600/3-78-020:45 pp.
BRITTAIN, J.E.   1976.   The temperature of two Welsh lakes and its effects on the distribution of two freshwater insects. Hydrobiologia 48:37-49.
BROOKER, M.P. AND R.J. HEMSWORTH.   1979.   The effect of the release of an artificial discharge of water on invertebrate drift in the River Wye, Wales. Hydrobiologia 59:155-163.
BRUNDIN, L.   1966.   Transantarctic relationships and their significance as evidenced by chironomid midges. Kungl. Svenska. Vetenskupacad. Handl. 11:1-472.
COFFMAN, W.P.   1973.   Energy flow in a woodland stream ecosystem II. The taxonomic composition and phenology of the Chironomidae as determined by the collection of pupal exuviae. Arch. Hydrobiol. 71:281-322.
DANKS, H.V.   1978.   Some effects of photoperiod, temperature and food on emergence of three species of Chironomidae (Diptera). Can. Ent. 110:289-300.

DURBAN, J.K. 1981. Tobin Lake Fishery 1979, 17 years after impoundment. Sask. Fish. Lab. Tech. Report 81-5:147 pp.

FERGUSON, V.M. AND R.C. FOX. 1978. A comparison of aquatic insects in natural inlets with those in heated effluent from the OCONEE nuclear station — Littoral zone. J. Ga. Ent. Soc. 13:202-213.

FRALEY, J.J. 1979. Effects of elevated stream temperatures below a shallow reservoir on a cold water macroinvertebrate fauna. p. 257-272. *In:* Ecology of Regulated Streams. J.V. Ward and J.A. Stanford (editors). Plenum Press, New York and London. 398 pp.

GOODNO, E.J. 1975. Post-impoundment limnology of the East Lynn Lake tailwater, West Virginia. Proc. West Vir. Acad. Sci. 47:170-176.

GORE, J.A. 1980. Ordinational analysis of benthic communities upstream and downstream of a prairie storage reservoir. Hydrobiologia 69:33-44.

HILSENHOFF, W.L. 1971. Changes in the downstream insect and amphipod fauna caused by an impoundment with a hypolimnion drain. Ann. Ent. Soc. Amer. 64:743-746.

LACKEY, R.T. 1973. Bottom fauna changes during artificial reservoir destratification. Wat. Res. 7:1349-1366.

LANGEFORD, T.E. 1975. The emergence of insects from a British River, warmed by power station cooling-water Part II. The emergence patterns of some species of Ephemeroptera, Trichoptera and Megaloptera in relation to water temperature and river flow, upstream and downstream of the cooling-water outfalls. Hydrobiologia 47:91-133.

LANGEFORD, T,.E. AND J.R. DUFFERN. 1975. The emergence of insects from a British River, warmed by power station cooling-water Part I. The use and performance of insect emergence traps in a large spate-river and the effects of various factors on total catches, upstream and downstream of the cooling-water outfalls. Hydrobiologia 46:71-114.

LAVILLE, H. 1979. A study of the drift of pupal exuviae of chironomids at the confluence of the Truyere and the River Lot. Ann. Limnol. 15:155-180.

LEHMKUHL, D.M. 1972. Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. J. Fish. Res. Board Can. 29:1329-1332.

_____. 1979. Environmental disturbances and life histories: Principles and examples. J. Fish Res. Board. Can. 36:329-334.

LESAGE, L. AND A.D. HARRISON. 1980. The biology of *Cricotopus* (Chironomidae: Orthocladiinae) in an algal-enriched stream: Part I. Normal biology. Arch. Hydrobiol. Suppl. 57:375-418.

MACKEY, A..P. 1977. Species diversity of some larval Chironomidae (Diptera) communities in two rivers. Oikos 29:150-155.

MERKLEY, W.B. 1978. Impact of Red Rock Reservoir on the Des Moines River. p. 62-76. *In*: Current Perspectives on River-Reservoir ecosystems. E. Benfield Jr. (editor). N.A. Benthol. Soc., Springfield, Illinois.

NEWELL, R.L. AND G.W. MINSHALL. 1978. Life history of a multivoltiine mayfly, *Tricorythodes minutus*: an example of the effect of temperature on the life cycle. Ann. Ent. Soc. Amer. 71:876-881.

NIE, N.H., C.H. HULL, J.G. JENKINS, K. STEINBRENNER AND D.H. BENT. 1975. SPSS (Statistical Package for the Social Sciences), 2nd edition. McGraw-Hill, New York, New York. 675 pp.

NORDLIE, K.J. AND J.W. ARTHUR. 1981. Effect of elevated water temperature on insect emergence in outdoor experimental channels. Env. Poll. (Series A) 25:53-65.

OLSON, D.E. AND D.C. TARTER. 1974. A pre-impoundment investigations of Beech Fork Basin Twelvepole Creek, Wayne and Cabell counties West Virginia, U.S.A. Proc. West Vir. Acad. Sci. 46:231-236.

Rossaro, B. 1978. The taxonomic composition and phenology of the Orthocladiinae, Diptera, Chironomidae, in Po River near Caorso (Piacenza) as determined by analysis of pupal exuviae. Riv. Hydrobiol. 17:287-290.

Rossaro, B. and U. Ferrarese. 1980. A contribution to the knowledge of chironomids in Italy, including cluster analysis of presence-absence data and factor analysis with per cent composition of species in a stream. p. 203-208. *In*: Chironomidae, Ecology, Systematics, Cytology and Physiology. D.A. Murray (editor). Pergamon Press, Oxford and New York. 354 pp.

Royer, L.M. 1969. A limnological and Fisheries survey of Tobin Lake, an impoundment on the Saskatchewan River, 1966-67. Sask. Fish. Lab. Report 1969:85 pp.

Sawchyn, W.W. 1974. Tobin Lake. A study of water quality, sediments and benthos. Sask. Res. Coun. Report 1975:79 pp.

Spence, J.A. and H.B.N. Hynes. 1971. Differences in benthos upstream and downstream of an impoundment. J. Fish. Res. Board. Can. 28:35-43.

Ward, J.V. 1974. A temperature-stressed ecosystem below a hypolimnial release mountain reservoir. Arch. Hydrobiol. 74:247-275.

_____. 1976a. Effects of flow patterns below large dams on stream benthos: A review. *In:* Instream Flow Needs Symposium, Vol. II. J.F. Osborn and C.H. Allman (editors). Amer. Fish. Soc. 1976:235-253.

_____. 1976b. Effects of thermal constancy and seasonal temperature displacement on community structure of stream macroinvertebrates. pp. 302-307. *In:* Thermal Ecology II, G.W. Esch and R.W. McFarlane (editors). ERDA Symposium Series (CONF-750425).

Ward, J.V. and R.A. Short. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, U.S.A. Verh. Intern. Ver. Limnol. 20:1382-1387.

Ward, J.V. and J.A. Stanford. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal codification of regulated streams. p. 35-56. *In:* The Ecology of Regulated Streams. J.V. Ward and J.A. Stanford (editors). Plenum Publishing Corporation. 378 pp.

Wartinbee, D.C. 1976. Quantitative determination of chironomid emergence from enclosed channels in a small lotic ecosystem. Amer. Midl. Nat. 95:479-485.

_____. 1979. Diel emergence patterns of lotic Chironomidae. Freshwat. Biol. 9:147-156.

Williams, R.D. and R.N. Winget. 1979. Macroinvertebrate response to a flow manipulation in the Strawberry River, Utah (U.S.A.). p. 365-376. *In:* Ecology of Regulated Streams. J.V. Ward and J.A. Stanford (editors). Plenum Press, New York and London. 398 pp.

Wilson, R.S. 1979. Classifying rivers using chironomid pupal exuviae. p 209-216. *In*: Chironomidae, Ecology, Systematics, Cytology and Physiology. D.A. Murray (editor). Pergamon Press, Oxford. England. 354 pp.

_____. 1977. Chironomid pupal exuviae in the River Chew. Freshwat. Biol. 7:9-17.

Wilson, R.S. and P.L. Bright. 1973. The use of chironomid pupal exuviae for characterizing streams. Freshwat. Biol. 3:283-302.

Wilson, R.S. and J.D. McGill. 1977. A new method of monitoring water quality in a stream receiving sewage effluent, using chironomid pupal exuviae. Wat. Res. 11:959-962.

Young, W.C., D.H. Kent and B.G. Whiteside. 1976. The influence of a deep storage reservoir on the species diversity of benthic macroinvertebrate communities of the Guadalupe River, Texas, U.S.A. Tex. J. Sci. 27:213-224.

Cytogenetic Studies on *Chironomus plumosus* L. (Diptera, Chironomidae) from different Populations and their Experimental Hybrids

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ABSTRACT. — Chironomus plumosus egg masses were collected from populations in Lake Neuchatel (Switzerland), Lake Wohlen (Switzerland) and Deer Lake (Vancouver, Canada). The larvae reared in the laboratory, the crossing of adult midges (Neuchatel ♂♂ X Wohlen ♀♀; Neuchatel ♀♀ X Wohlen ♂♂; Vancouver ♂♂ X Wohlen ♀♀) were initiated artificially.

The analysis of the polytene chromosomes of 4th instar larvae leads to the following conclusions: The individuals from Neuchatel and Wohlen differed by several homozygous inversions, making them clearly distinguishable. Such inversions have been found in the chromosome arms A, B, C, D and G. Four inversions (in arm: A, B, C and D) are forming polymorphic systems in both populations. In hybrid larvae the pairing of the homologue chromosomes is not disturbed in sections with similar band sequences. The populations from Neuchatel and Wohlen are closely related. They can be considered as subspecies which diverged on the basis of inversions.

The difference between the populations of Vancouver and Wohlen are much more pronounced. We have found homozygous inversions in the arms B, D, E and G. In the hybrids, asynapsis of the homologue chromosomes is almost complete due to genic changes which are not reflected in the banding patterns. While the chromosomes of individuals from the Neuchatel and Wohlen populations have striking centromere regions, those of the Vancouver population have indistinct centromere regions. By means of the C-banding technique it could be established that in the European populations the heterochromatin is located mainly in the centromere regions, while in Vancouver population there is a considerable amount of heterochromatin in different parts of the chromosomes.

The differing display of C-bands in the initial populations and the hybrids (Vancouver X Wohlen) reveals a different gene regulation which was first reported for chironomus and polytene chromosomes in general. The Vancouver population is not only geographically distant from the European populations, the observed differences would even provide basis for the separation of the latter into an independent species.

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INTRODUCTION

The taxonomy of *Chironomus plumosus* has puzzled chironomid workers for many years. Some authors (Lenz, 1924; Tchernovski, 1948) considered it as a polytypic species: they distinguished several larval forms based on the length of the processes on the 8th larval segment. Keyl and Keyl (1959), Palmén and Aho (1969), Krieger and Wülker (1971) regarded *Ch. plumosus* as a species-complex incorporating several species with distinct ecological and cytological peculiarities. The comparative karyological studies of Michailova and Maximova (1980) on distant populations in USSR and Bulgaria showed that the species is in the process of divergence.

The aim of this study is to obtain new information on the taxonomic status of different populations of "the species" *Chironomus plumosus*. For this purpose we have analysed different populations cytotaxonomically: adjacent European (Neuchatel and Wohlen, Switzerland; Plovdiv and Durankulak, Bulgaria) as well as geographically distant populations (Switzerland/Bulgaria/Canada). We also analysed hybrids between different populations. This will contribute to our knowledge on interpopulational relationships, the taxonomic status and the steps of evolution within the particular populations. As the species divergence causes not only karyotype differences but also differences in number, size and localization of the constitutive heterochromatin blockes (Gatti, Pimpinelli, Sautini, 1976), the distribution and localization of the constitutive heterochromatin in individuals from the natural populations and in hybrids were determined by C banding technique.

For each population a cytological map was made in which the chromosomes are indexed by letters, and the sections within the chromosomes by digits.

In this paper we will discuss only the results concerning the populations from Neuchatel, Wohlen and Vancouver. The Bulgarian populations will be discussed later.

MATERIAL AND METHODS

Adult midges in the process of laying egg masses were collected on the shores of Lake Neuchatel (Switzerland), Lake Wohlen (Switzerland) and Deer Lake (Vancouver/Canada). The lake Neuchatel is a large mesotrophic lake with a sandy sediment. Lake Wohlen is a reservoir formed by damming the river Aare; due to still considerable water flow it does not stratify. The sediment consists of a thick layer of silt. The Deer Lake is a small, highly eutrophic lake without current; the sediment is similar to that of Lake Wohlen.

The larvae hatching from the collected egg masses were reared in laboratory in containers of 1-101, using dechlorinated tap water. The substrate consisted of cellulose fibers and sterilized sediment from Lake Wohlen. The larvae were fed with minced Tetra Phyll flakes (Tetra-Werke, Melle, Western Germany). The crossings of adult midges were made by a method described earlier (Fischer, 1969).

The staining methods (Aceto-Orceine and C-banding) also have been described earlier (Valkanov and Michailova, 1974; Michailova and Maximova, 1980).

RESULTS AND DISCUSSION

The adults and larvae from the natural populations and all hybrid forms could not be distinguished morphologically. The analysis of the polytene chromosomes of the 4th instar larvae leads to the following conclusions: in
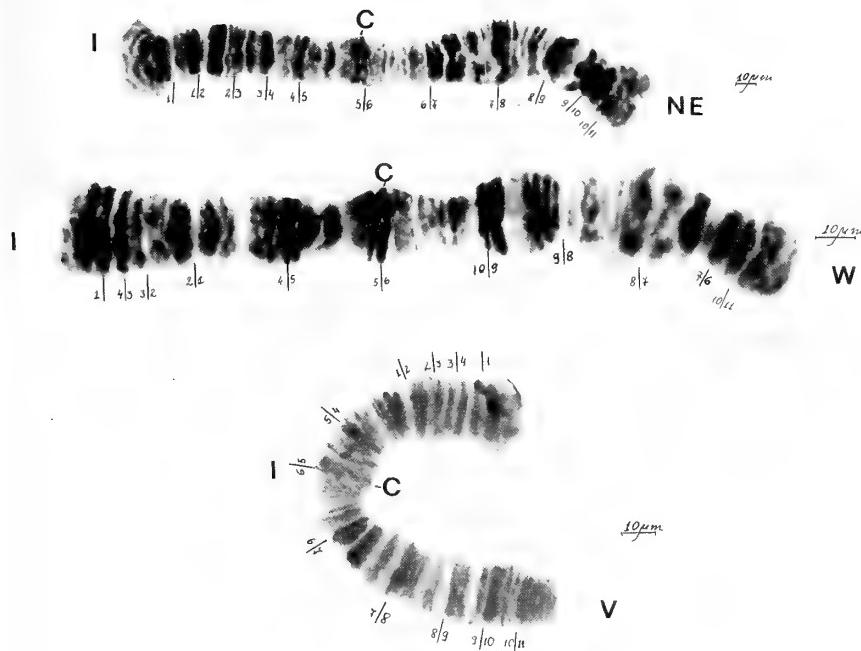
FIG. 1a. Chromosome I of initial populations (Neuchatel, Wohlen and Vancouver). Ne-Neuchatel; W-Wohlen, V-Vancouver.
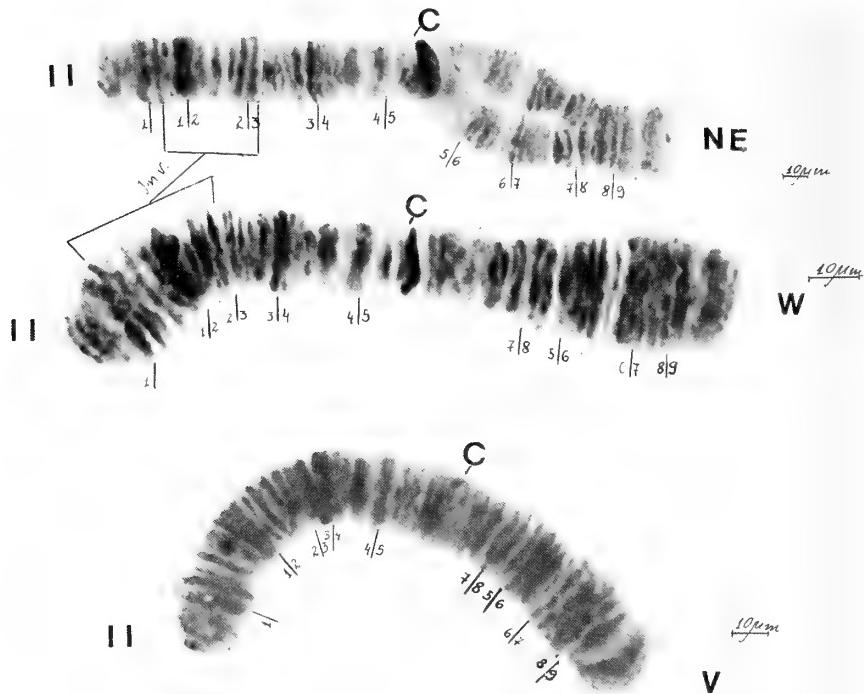
FIG. 1b. Chromosome II of initial populations (Neuchatel, Wohlen and Vancouver). Ne-Neuchatel; W-Wohlen, V-Vancouver.

all investigated populations, the 1st, 2nd and 3rd chromosomes are meta-centric, the 4th is acrocentric.

Each of the natural populations has its characteristic pattern of inversions and other rearrangements (Fig. 1a, b, c, d), making them clearly distinguishable. Comparing individuals from Neuchatel and Wohlen, inversions have been found in the chromosome arms A, B, C, D and G. Four inversions (in arms A, B, C and D) are forming polymorphic systems in both populations. Comparing the populations of Vancouver and Wohlen, we have found inversions in the arms B, D, E, and G. In the Vancouver population, polymorphic systems do not seem to exist. The polytene chromosomes of hybrids can differ considerably from those of their parents: while in the parents the homologue chromosomes conjugate along their entire length with very rare incomplete pairing, the pairing in the hybrids can be disturbed. In this repect, the two investigated types of hybrids differed fundamentally.
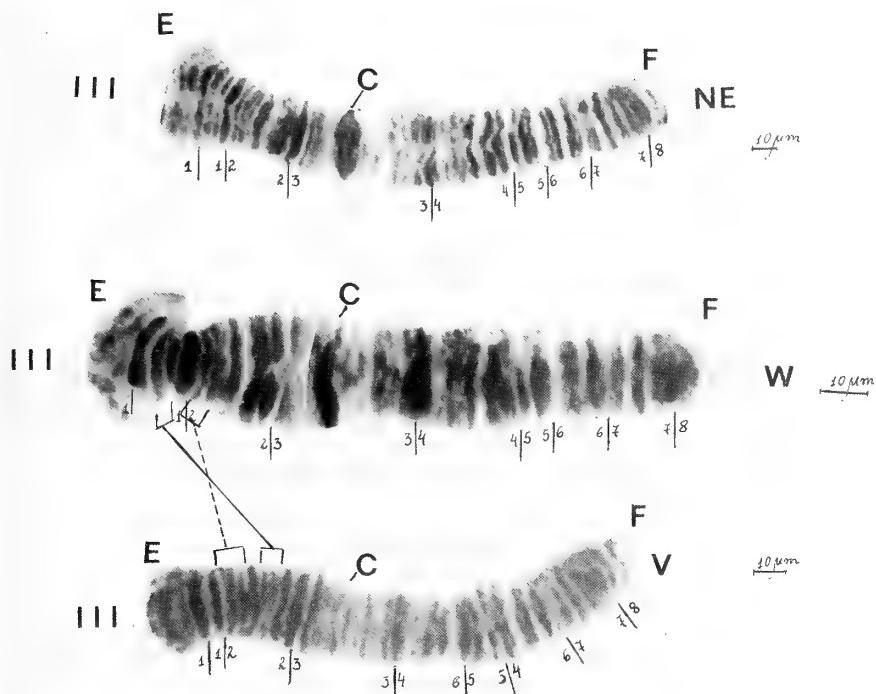
Fig. 1c. Chromosome III of initial populations (Neuchatel, Wohlen and Vancouver). Ne-Neuchatel, W-Wohlen, V-Vancouver.

In the hybrids Neuchatel X Wohlen, the homologue chromosomes are paired in sections with similar band sequences. In some sections inversions cause the formation of inversion loops (Fig. 3). The 3rd chromosomes of the two populations have identical banding patterns; here, in most cases, we have found complete synapsis in the hybrids (Fig. 4). The rare occurrence of asynapsis can be explained by the theory of heterocyclicity of father's and mother's chromosomes (Prokofyeva-Belgovskaya, 1946). The different stages of these chromosomes are evident from the staining intensity of the homologous bands, their thickness and alterations in the band sequence of the homologue. The most interesting feature of the combination Vancouver ♂ X Wohlen ♀ is that, even in case of apparently identical banding pattern, the homologues of all the chromosomes are strongly asynaptic. For example: in the 1st chromosome, synapsis occurs usually only between section 4/5-5/6 and several bands after 5/6 (Fig. 2). In the 2nd chromosome, synapsis can be observed usuallly in the first part of the chromosome (Fig.
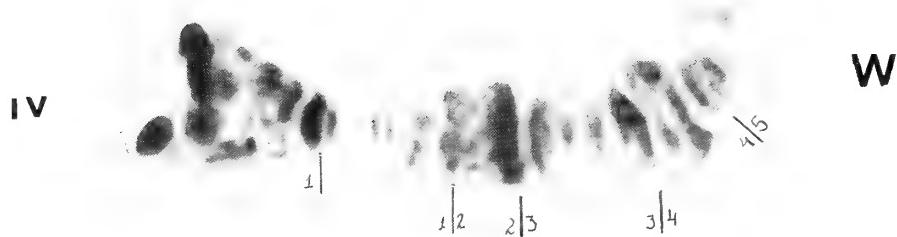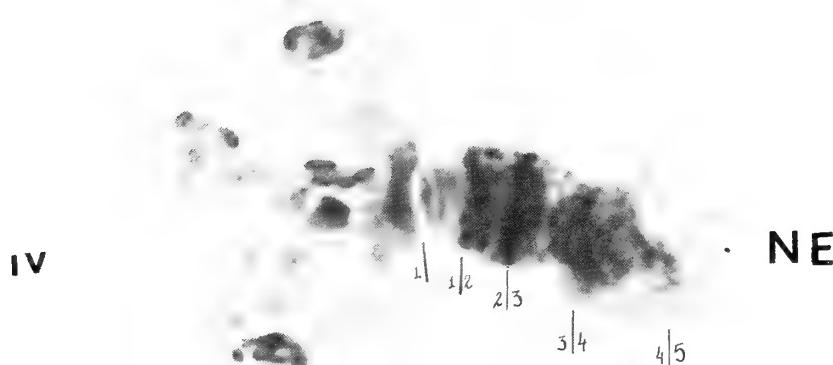
5). The homologues of the 3rd chromosome usually are completely separated (Fig. 6). The homologues of the 4th chromosome also are completely separated in hybrids, but the same can be observed also in individuals from natural populations.

It appears that various factors are involved in the phenomenon of chromosomal pairing. The cases of asynapsis can be divided into three groups:

1. The homologue chromosomes have identical banding patterns. In this case the absence of pairing must be caused by differences on the molecular (at least submicroscopic) level.
2. The banding patterns of the two homologue chromosomes are not identical: each homologon shows the parental arrangement.
3. One homologon has a clear banding pattern and the other shows some grain structure. This kind of asynapsis can be explained by the theory of heterocyclity of the father's and mother's chromosomes (Prokofyeva-Belgovskaya, 1946).

To date, it is not clear what causes some tissues in certain organisms to grow by endomitosis and form polytene chromosomes. It also is not known which chromosome structures are responsible for the synapsis. Such structures ("synaptomeres") must exist (Nagl, 1972). We have not much information about them, but we can assume that they differ fundamentally from normal genes when considering ecological-genetical aspects of populations. As opposed to other genes, the synaptomeres cannot be affected by environmental selection factors. Therefore one might consider the synaptomeres to evolve at a higher rate than genes which are responsible for morphological or physiological features. Consequently, the lack of homologue pairing in hybrids should be one of the first visible differences between independently evolving populations.

The different behaviour of the homologue chromosomes in the two types of hybrids (Neuchatel X Wohlen; Wohlen X Vancouver respectively) indicates that the two geographically adjacent populations are also biologically closely related, while the geographically distant populations are distant biologically. The application of C-banding technique shows that the studied populations diverge also on the basis of amount and distribution of constitutive heterochromatin, which indicates some functional differences. In the Neuchatel and Wohlen individuals the heterochromatin is located in the centromere regions of the 1st, 2nd and 3rd chromosomes (in the Wohlen

Fig. 1d. Chromosome IV of initial populations (Neuchatel, Wohlen and Vancouver). Ne-Neuchatel, W-Wohlen, V-Vancouver.

2

3

4

5

V   W

6

7

8

10 μm
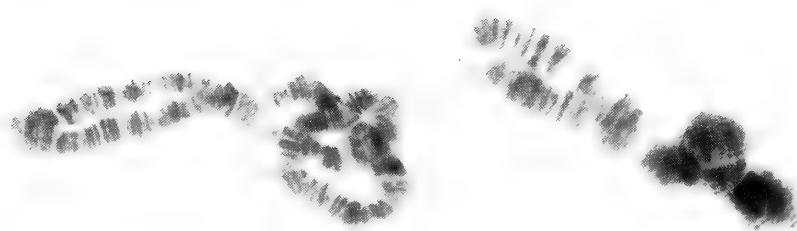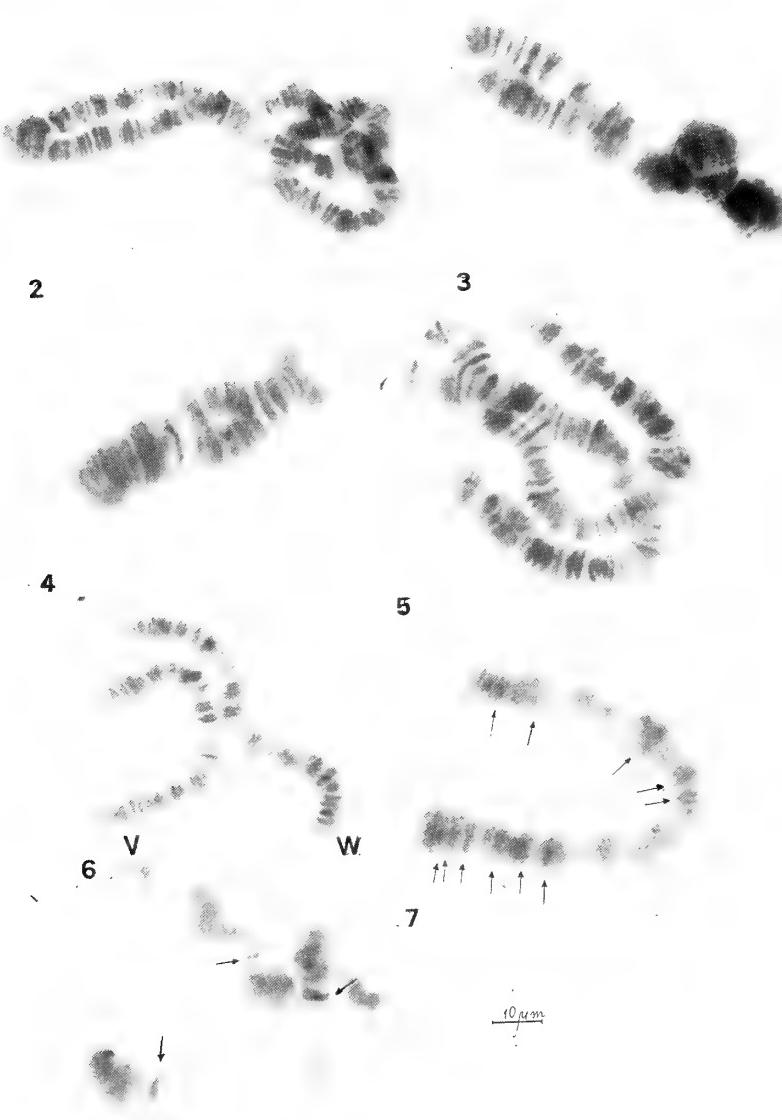
population also a few in the bands 1/2, 8/9 of the 2nd chromosome), while in the Canadian population there is a considerable amount of heterochromatin distributed over the whole chromosomes (Fig. 7).

In the hybrid (Neuchatel X Wohlen) only a few bands and the centromere regions are heterochromatic (Fig. 8). The reverse is the case with the hybrids Vancouver X Wohlen which show numerous C-bands, i.e., numerous genes are repressed, while in the parental forms there are only a few heterochromatic regions. C-bands were found in the hybrids Vancouver X Wohlen as follows:

1st chromosome, father's homologon (Vancouver): sections 1, 4/3, 3/2, 2/1, 5/6, 6/7, 8/9, 10/11.

1st chromosome, mother's homologon (Wohlen): section 1, 4/3, 3/2, 9/10.

2nd chromosome, father's homologon: entire arm C and sections 7/8, 5/6, 6/7.

2nd chromosome, mother's homologon: entire arm C and sections 7/8, 5/6, 8/9.

3rd chromosome, father's homologon: sections 1, 1/2, 3/4, 4/5, 6/7.

3rd chromosome, mother's homologon: centromere region and section 2/3.

4th chromosome: both homologons: sections 2/3, 3/4, 4/5.

When considering the relationship of populations, it would be interesting to compare also the mating behaviour. Unfortunately it has not been possible till now to induce swarming and normal mating behaviour of our populations of *Ch. plumosus* in the laboratory. In our work, the crossing was initiated artificially. Therefore, any possible ethological isolation factors were bypassed. Another interesting question is the behaviour of hybrid chromosomes in meiosis. For this purpose, we intend to analyse larvae derived from back-crossing.

CONCLUSIONS

Hybridization tests and cytogenetic analysis prove experimentally that "the species" *Chironomus plumosus* is in the process of divergence to a

FIGS. 2-8.   2. Chromosome I of a hybrid (Vancouver ♂ X Wohlen ♀) with asynapsis and a complex heterozygous inversion; 3. Chromosome I of a hybrid (Neuchatel ♂ X Wohlen ♀); 4. Chromosome III of a hybrid (Neuchatel ♂ X Wohlen ♀); 5. Chromosome II of a hybrid (Vancouver ♂ X Wohlen ♀); 6. Chromosome III of a hybrid (Vancouver ♂ X Wohlen ♀); 7. C-bands of chromosome I of Canadian Population; 8. C-bands of chromosomes I, II and III of a hybrid Neuchatel ♂ X Wohlen ♀.

varying extent in different regions of its distribution area. The constant high level of synapsis between hybrid homologues in the combination Neuchatel X Wohlen indicates that the two Swiss populations are closely related and diverged only on the basis of chromosome aberrations.

The Canadian population is more distant phylogenetically. Asynapsis of homologue chromosomes is almost complete in hybrids Vancouver X Wohlen due to genic changes which are not reflected in the banding patterns. The genic alterations have accumulated during the evolution to such an extent that normal synapsis in the hybrids is no longer possible. These genic differences, together with the dissimilar arrangement of heterochromatin and the different homozygous inversions would provide basis for the separation of the Canadian population into an independent species. The different arrangement of C-bands in the initial populations and the hybrids (Vancouver X Wohlen) indicates a different gene regulation, a fact new for Chironomus and polytene chromosomes in general.

REFERENCES

FISCHER, J. 1969. Zur Fortpflanzugsbiologie von *Chironomus nuditarsis*. Rev. suisse Tool. 76:23-55.

GATTI, N., S. PIMPINELLI AND G. SAUTINI. 1976. Characterization of *Drosophila* Heterochromatin. 1. Staining and Decondensation with Hoest 332558 and Quinacrine. Chromosoma. 57:351-371.

KEYL, H.G. AND I. KEYL. 1959. Die cytologische Diagnostik der Chironomiden. I. Bestimungstabelle für die Gattung *Chironomus* auf Grund der Speicheldrüsen Chromosomen. Arch. f. Hydrobiol., 56:43-57.

KITZMILLER, J., G. FRIZZI AND W. BAKER. 1967. Evolution and Speciation within the *maculipennis* Complex of the Genus *Anopheles*. Genetics of Insect Vectors of Disease. 151-208.

KRIEGER-WOLF, E. AND W. WÜLKER. 1971. Chrionomiden (Diptera) aus der Umgebung von Freiburg i. Br./mit besonderer Berücksichtigung der Gattung *Chironomus*/Beitr. natural. Forsch. Sud. d. W. DTL. 30:133-145.

LENZ, F. 1924. Die Chironomiden der Wolga. Arb. Biol. Wolga-Station. 3:97-126.

MICHAILOVA, P. AND F. MAXIMOVA. 1980. Karyological Variability of *Chironomus plumosus* L. (Diptera: Chironomidae) and its Importance for the Species Divergence. Acta Zoologica Bulgarica. 14:5-18.

NAGL, W. 1972. Chromosomes. Wilhelm Goldmann Verlag München.

PALMEN, E. AND L. AHO. 1966. Studies on the Ecology and Phenology of the Chironomidae of the Northern Baltic. 2. *Camptochironomus* Kieff. and *Chironomus* Meig. Annali Zool. Fenn. 3:217-244.

PROKOFYEVA-BELGOVSKAYA, A.A. 1946. Heterocyclicity of the Parental Chromosomes set. Comp. Rendus de l' Academy Sciences de l' USSR. 2:18-25.

TCHERNOVSKII, A.A. 1949. Key of the Larvae of the Fam. Tendipedidae. USSR.

VALKANOV, A. AND P. MICHAILOVA. 1974. Untersuchungen über den Karyotypus und Chromosomenpolymorphism bei *Thalassomyia frauenfeldi* Schiner (Diptera, Chrionomidae) von der bulgarischen Schwarzmeerküste. Bull. Inst. Zool. Mus. 40:5-16.

An Inventory of the Irish Chironomidae (Diptera)

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ABSTRACT. — The resident Irish biota is poor in species in comparison with that of Britain and mainland Europe. Only two thirds of the native British flora occurs naturally in Ireland and the native Irish fauna is similarly poor in species. Studies on the Irish Chironomidae in recent years have shown that approximately 347 species are now known to occur. An inventory of these species is given in this paper. To date 69% and 29% respectively of the western Palaearctic genera and species and 70% of the species known from Britain have been recorded from Ireland.

INTRODUCTION

The family Chironomidae is represented by approximately 1400 species in 186 genera in the 25 European zones of the western Palaearctic region recognised by Illies in Limnofauna Europaea (Illies, 1978: Fittkau and Reiss 1978).

Since the publication of the list of Chironomidae in Ireland (Murray 1972) additional records have been given by Fahy and Murray (1972); Murray (1976a,b); Pinder and Cranston (1976); Douglas and Murray (1980); Dowling et al (1981); Dowling and Murray (1981); Murray and O'Connor (1982) and Murray and Ashe (1982).

Lists of species are a "neglected mine of valuable information whose exploitation should do much to clarify the zoogeographical and ecological components of animal distribution" (Blackith and Blackith 1975). Compilation of such lists forms a basic and important component of ecological research and there still exists a need for continued effort in this field of chironomid research in many countries, including Ireland. The need is all the more pressing with the realisation that many habitats are being steadily eroded and damaged not only by natural forces but also through human neglect, exploitation, pollution and other aspects of 20th century life. An inventory of the Chironomidae currently known to occur in Ireland, zone 17 of Limnofauna Europea (Illies l.c.), is given in Table 1. This list incorporates the records of the last decade and includes corrections of some species names from the previous list (Murray 1972) which have been necessitated as a result of recent taxonomic revisions. Previously unpub-

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lished records are denoted by an asterisk"*". Distributional data of these latter species in Ireland is given in Ashe, Hayes and Murray (in prep.).

Included in the list are some species records which require comments.

Anatopynia plumipes (Fries)

This monospecific genus is known only from middle and northern Europe. Larvae live, according to Brundin (1949), in the littoral region of small lakes and ponds. Fittkau (1962) regards it as a rare species. The record of this species from Ireland, based on a mature male pupa, is in general agreement with previous ecological information but its emergence, in March, is three/four weeks earlier than previously reported.

Telmatopelopia nemorum (Goetgh.)

This doubtful record is based on a single female taken by Fahy (Fahy and Murray l.c.). The material has since been mislaid and there have been no additional records in the interim period.

Diamesa permacer (Walk.)

The adult male of this rare palaearctic species, collected by C.F. Humphries in 1950 near Dublin, is to be found in the British Museum of Natural History, London. The material had been sent to Dr. P. Freeman for identification and the specimen in question had obviously been reared from the larva since both larval and pupal exuviae have recently been located in the slide collection made by Humphries and now on deposit in the Zoology Department, University College, Dublin.

Bryophaenocladius virgo Thien.

This record is based on the identification of a single pupal exuviae (leg. Ashe) from the River Flesk, Killarney. Morphological characters of the specimen agree entirely with the descriptions given by Strenzke (1950) but there remain a number of species in this genus whose pupa is, as yet, unknown.

Georthocladius luteicornis (Goetgh.)

Larvae of this monospecific genus have previously only been found in moist or wet turf or bog biotopes. The single pupal exuviae recorded from the River Flesk (leg. Ashe) in all probability originated from moist soil above the river bank. The species is not known from Britain.

Orthocladius (Euorthocladius) ? rusticus Goetgh.

For some time now a characteristic *Euorthocladius* pupal exuviae, differing from descriptions of the existing species, has been known to the authors. Associated adults resemble *O. (E.) thienemanni* Kieff. The pupal abdominal chagrin on the posterior edge of tergites IV-VIII and the three dor-

socentral setae on the thorax are much more robust in comparison with those on the other members of the genus. This species has been collected in numerous rivers in Ireland (leg. Murray, Ashe) and is also known from two locations in Norway and one in France (leg. Murray). Recent examinations of slide material prepared by C.F. Humphries has revealed that reared material had been sent by her to Goetghebuer for identification. Some slides in Humphries' collection are labelled "*O. rusticus*". The possibility therefore exists that Goetghebuer identified the associated male and communicated this information to Humphries. It is not possible to state at this time whether the specimens belong to *O. rusticus* or to a new species.

Orthocladius (O.) dentifer Brundin and *O. (Pogonocladius) consobrinus* (Holm.)

The record of *O. dentifer* is based on a re-examination of some material of *O. (Pogonocladius) consobrinus* made available by Murray to Dr. P. Cranston (Pinder and Cranston, 1976). To date this is the sole record of *O. dentifer* from Ireland or Britain. *O. (P.) consobrinus* has been recorded from four Irish locations. It is predominantly a late winter/spring emerging species. Pupal exuviae have been collected from lake surfaces during January/February.

Rheosmittia spinicornis Brund.

Pupal exuviae of this species have been obtained from the River Slaney in S.E. Ireland (leg. Hayes). Only two species are known in the genus neither of which occur in Britain. The pupa is readily identifiable on the basis of the characteristic palmate abdominal setae.

Harnischia falcata Kieff.

This species was recorded in Limnofauna Europaea (Fittkau and Reiss, l.c.). The original source of the record is unknown to the present authors.

Microchironomus deribae (Freem.).

Damaged adults of this species were obtained from the fuel filtering system of a helicopter based at the Baldonell military airport near Dublin. The validity of including the record as part of the Irish fauna is questionable as the helicopter had been refueled in France some time prior to the discovery of the insects in the filter (Murray and O'Connor 1982).

Corynocera ambigua Zett.

Adult males and females of this brachypterous species have recently been taken from L. Corrib (leg. Connolly) a large limestone lake in western Ireland. *C. ambigua* has a predominantly boreal distribution and is not yet recorded from Britain.

Our current knowlege of the Irish Chironomidae shows that 347 species in 128 genera are known to occur (Table 2). This compares with 460 species and 133 Genera in Britain and approximately 1200 species and 186 genera in Europe. Approximately 38% of the European chironomid species has been recorded from Britain while only 29% has so far been recorded from Ireland. Three hundred and twenty seven species on the Irish list are known from Britain. It is noteworthy, however, that some species on the Irish list, including those belonging to the genera *Anatopynia, Georthocladius, Rheosmittia* and *Corynocera,* are not yet recorded from Britain. Conversely there are fourteen genera and some 158 species found in Britain which have not been recorded from Ireland. Approximately 70% of the species known from Britain are also recorded in Ireland. This trend compares favourably with records for two other insect groups with aquatic life stages since only 73% and 62% of the Trichoptera and Ephemeroptera respectively, recorded in Britain are known from Ireland. (Table 3).

DISCUSSION

Absence of a taxon from the faunal list of a particular area is, according to Blackith and Blackith (1975), attributed to two clear propositions: that the members of the taxon never reached the area in question or, if they did, were unable to maintain a permanent population. It must be recognised, however, that the content and length of national or regional faunal lists also reflects the intensity of sampling and variety of habitats sampled. Thus rare species may remain undetected for years.

The flora and fauna of the island of Ireland, lying to the west of mainland Europe and separated from its nearest neighbour Britain by the Irish sea, is characterised by a lower number of species than that of Britain or Europe. Only two thirds of the native British Flora occurs naturally in Ireland and likewise Ireland contains only one third of the reptiles and half of the land mammals found in Britain (Mitchell 1976). It has been postulated that events during and after the last glaciation have led to this situation. Many authors believe that the plants and animals now present in Ireland are post-glacial immigrants as it is suggested that few could have survived at maximum glaciation (Healy 1979). The route for the floral and faunal recolonisation of Ireland from Europe lay through Britain but as sea levels rose on the retreat of ice the land bridge between Britain and Ireland was severed long before Britain was isolated from the continent (Mitchell 1976) thus establishing a barrier to dispersal. Whereas this scenario might validly apply to the terrestrial fauna using land bridges as dispersal routes it need not necessarily apply to insects with the ability to fly. It would seem

that there has been ample time in the 10,000 years since glaciation for most European invertebrate species to have reached Ireland but the fact remains that the Irish fauna does appear impoverished in relation to Britain's. The lack of ecological variety has been cited as a possible factor to explain the low number of species in Ireland's fauna (Healy l.c.).

Ireland lacks the extensive areas of dry heath or chalkland and is deficient in deciduous woods in comparison with Britain but in relation to the aquatic insects this need not necessarily present a serious obstacle. Nevertheless all the available data indicates that the Irish chironomid fauna exhibits a trend similar to other freshwater groups and undoubtedly appears impoverished in comparison with Britain.

Keeping in mind the fact that the length of faunal lists is partly a reflection of the intensity of work done on a particular group it is anticipated that the number of species on the Irish Chironomid list will increase in the years ahead. For example little work has been done to date on the semi-aquatic chironomids in Ireland. Likewise it is highly probable that many of the species recorded in Ireland and not yet reported from Britain will eventually be found there.

It is suggested that a combination of geographical isolation and the prevailing westerly/south-westerly Atlantic winds have constituted effective barriers preventing largescale immigration. The presence of some species with a boreal distribution may additionally support a theory that local refugia existed to allow some species survive maximum glaciation.

REFERENCES

BLACKITH, R.E. AND R.M. BLACKITH. 1975. Zoogeographical and ecological determinants of Collembolan distribution. Proc. R. Ir. Acad. 75B 18:345-368.

BRUNDIN, L. 1949. Chironomiden und andere Bodentiere der sudschwedischen Urgebirgssen. Rep. Inst. Freshwat. Res. Drottingholm. 30:1-914.

DOUGLAS, D.J. AND D.A. MURRAY. 1980. A Checklist of the Chironomidae (Diptera) of the Killarney Valley Catchment, pp 123-130. In MURRAY, D.A. (Ed.): Chironomidae-Ecology, Systematics, Cytology and Physiology. Pergamon Press, Oxford, 354 pp.

DOWLING, C. AND D.A. MURRAY. 1981. The distribution of the Chironomidae (Diptera) in two Irish blanket bogs. Proc. R. Ir. Acad. 81B:53-61.

DOWLING, C., J.P. O'CONNOR AND M.F. O'GRADY. 1981. A baseline survey of the Caragh, an unpolluted river in southwest Ireland: Observations on the macro-invertebarates. J. Life Sci. R. Dubl. Soc. 2:147-159.

FAHY, E. AND D.A. MURRAY. 1972. The Chironomidae from a small stream system in western Ireland with a discussion of species composition of the group (Diptera). Entomol. Ts. 93:148-155.

FITTKAU, E.J. 1962. Die Tanypodinae (Diptera, Chironomidae). Abh. Larvalsyst. Insekten, 6:1-453.

FITTKAU, E.J. AND F. REISS. 1978. Chironomidae, pp 404-444. In J. Illies (Ed.) Limnofauna Europaea, 2nd. edn. Gustav Fischer Verlag, Stuttgart, 534 pp.

HEALY, B.   1978.   Records of Enchytraeidae (Oligochaeta) in Ireland. J. Life Sci. R. Dubl. Soc. 1:39-70.

ILLIES, J.   1978.   Limnofauna Europaea. 2nd. edn. Gustav Fischer Verlag, Stuttgart, 532 pp.

MITCHELL, F.   1976.   The Irish Landscape. Collins, London.

MURRAY, D.A.   1972.   A list of the Chironomidae (Diptera) known to occur in Ireland with notes on their distribution. Proc. R. Ir. Acad. 72B:275-293.

————————.   1976a.   *Buchonomyia thienemanni* Fitt. a rare and unusual species (Diptera, Chironomidae) recorded from the Killarney area, Ireland. Ent. Gaz. 27;

————————.   1976b.   *Thienemannimyia pseudocarnea* n.sp. a palaearctic species of the Tanypodinae (Diptera, Chironomidae). Ent. Scand. 7:191-194.

MURRAY, D.A. AND P. ASHE.   1982.   First Records of the subfamilies Podonominae and Telmatogetoninae (Diptera, Chironomidae) from Ireland. Ir. Nat. J. 22:546-547.

MURRAY, D.A. AND J.P. O'CONNOR.   1982.   *Microchironomus deribae* (Freem.) (Diptera, Chironomidae) a fuel contaminant in an Irish helicopter. Ent. Mo. Mag. 118:44.

PINDER, L.C.V. AND P.S. CRANSTON.   1976.   Morphology of the male imagines of *Orthocladius (Pogonocladius) consobrinus* and *O. Glabripennis* with observations on the taxonomic status of *O. glabripennis*. Ent. Scand. 7:19-23.

STRENZKE, K.   1950.   Systematik, Morphologie, und Okologie der terrestrischen Chironomiden. Arch. Hydrobiol. (Suppl) 18:207-414.

TABLE 1.   Chironomidae recorded from Ireland. Previously unpublished records denoted by*

TANYPODINAE
Ablabesmyia longistyla Fitt.
A. monilis (L.)
A. phatta (Egg.)
*Anatopynia plumipes (Fries)
*Apsectrotanypus trifascipennis (Zett.)
Arctopelopia barbitarsis (Zett.)
A. griseipennis (Wulp)
Clinotanypus nervosus (Meig.)
Conchapelopia melanops (Wied.)
C. pallidula (Meig.)
C. viator (Kieff.)
Guttipelopia guttipennis (Wulp)
Krenopelopia binotata (Wied.)
K. nigropunctata (Staeg.)
Larsia atrocincta (Goetgh.)
L. curticalcar (Kieff.)
Macropelopia goetghebueri Kieff.
M. nebulosa (Meig.)
M. notata (Meig.)
Monopelopia tenuicalcar (Kieff.)
Natarsia nugax (Walk.)
N. punctata (Fabr.)
Nilotanypus dubius (Meig.)
Paramerina cingulata (Walk.)
P. divisa (Walk.)

Procladius (Procladius) barbatus Brund.
P. (P.) choreus (Meig.)
P. (P.) crassinervis (Zett.)
P. (P.) culiciformis (Linn.)
P. (P.) sagittalis Kieff.
P. (P.) signatus (Zett.)
P. (P.) simplicistilus Freem.
P. (P.) sp. cf. crassinervis (Zett.)
Procladius (Psilotanypus) albinervis (Kieff.)
P. (Ps.) flavifrons Edw.
P. (Ps.) lugens Kieff.
P. (Ps.) ruffovittatus (Wulp)
Psectrotanypus varius (Fabr.)
Rheopelopia eximia (Edw.)
R. maculipennis (Zett.)
*R. ornata (Meig.)
Tanypus punctipennis (Meig.)
Telmatopelopia nemorum (Goetgh.)
Thienemannimyia carnea (Fabr.)
T. laeta (Meig.)
T. lentiginosa (Fries)
T. northumbrica (Edw.)
T. pseudocarnea Murray
Trissopelopia longimana (Staeg.)
Xenopelopia falcigera (Kieff.)

X. nigricans Fitt.
*Zavrelimyia barbatipes (Kieff.)
Z. hirtimana (Kieff.)
Z. melanura (Meig.)
Z. nubila (Meig.)

PODONOMINAE
Parochlus kiefferi (Garrett)

BUCHONOMYIINAE
Buchonomyia thienemanni Fitt.

PRODIAMESINAE
Monodiamesa bathyphila Kieff.
Prodiamesa olivacea (Meig.)
P. ruffovittata (Goetgh.)

DIAMESINAE
Diamesa bohemani Goetgh.
D. chiron (Hal.)
D. cinerella (Meig.)
D. incallida (Walk.)
D. insignipes Kieff.
*D. permacer (Walk.)
D. thienemanni Kieff.
Potthastia gaedii (Meig.)
P. longimana Kieff.
P. montia (Edw.)
Protanypus morio (Zett.)
Pseudodiamesa branickii (Now.)
P. nivosa (Goetgh.)

TELMATOGETONINAE
Thalassomya frauenfeldi Schin.

ORTHOCLADIINAE
Acricotopus lucens (Zett.)
Brilla longifurca Kieff.
B. modesta (Meig.)
Bryophaenocladius furcatus (Kieff.)
B. nitidicollis (Goetgh.)
*B. subvernalis (Edw.)
*B. virgo Thien.
Camptocladius stercorarius (deGeer)
Cardiocladius fuscus Kieff.
Chaetocladius dentiforceps (Edw.)
*C. perennis (Meig.)
Clunio marinus Hal.
Corynoneura carriana (Edw.)

C. celeripes (Winn.)
C. celtica Edw.
C. coronata (Edw.)
C. edwardsi Brund.
*C. lacustris Edw.
C. lobata Edw.
C. scutellata Winn.
*Cricotopus (C.) albiforceps (Kieff.)
C. (C.) annulator Goetgh.
C. (C.) bicinctus (Meig.)
C. (C.) curtus Hirv.
*C. (C.) epipphium (Zett.)
C. (C.) festivellus (Kieff.)
C. (C.) fuscus (Kieff.)
C. (C.) pulchripes Verr.
C. (C.) similis Goetgh.
C. (C.) tremulus (L.)
C. (C.) triannulatus (Macq.)
C. (C.) trifascia Edw.
*C. (C.) tristis Hirv.
C. (Isocladius) laricomalis Edw.
C. (I.) ornatus (Meig.)
C. (I.) reversus Hirv.
C. (I.) sylvestris (Fabr.)
C. (I.) tricinctus (Meig.)
C. (I.) trifasciatus (Meig.)
C. (Nostococladius) lygropis Edw.
*Diplocladius cultiger Kieff.
Epoicocladius flavens (Mall.)
Eukiefferiella brevicalcar (Kieff.)
E. claripennis (Lund.)
E. clypeata Kieff.
E. coerulescens Kieff.
E. devonica (Edw.)
E. dittmari Lehm.
E. gracei (Edw.)
E. ilkleyensis (Edw.)
E. minor (Edw.)
Eurycnemus crassipes (Panz.)
*Georthocladius luteicornis (Goetgh.)
Gymnometriocnemus brumalis Edw.
*Halocladius (Halocladius) fucicola (Edw.)
H. (H.) variabilis Staeg.
H. (H.) varians (Staeg.)
H. (Psammocladius) braunsi (Goetgh.)
Heleniella ornaticollis (Edw.)
Heterotanytarsus apicalis (Kieff.)
Heterotrissocladius grimshawi (Edw.)
H. marcidus (Walk.)

*Krenosmittia camptophleps (Edw.)
Limnophyes exiguus (Goetgh.)
L. gurgicola Edw.
L. minimus (Meig.)
L. prolongatus (Kieff.)
L. truncorum Goetgh.
Metriocnemus atriclavus (Kieff.)
M. fuscipes (Meig.)
M. hirticollis (Staeg.)
M. hygropetricus Kieff.
M. picipes (Meig.)
*Nanocladius (Nanocladius) balticus (Palm.)
N. (N.) bicolor (Zett.)
*N. (N.) rectinervis (Kieff.)
Orthocladius (Eudactylocladius) femineus
    (Edw.)
O. (Euorthocladius) rivicola (Kieff.)
O. (E.) rivulorum (Kieff.)
O. (E.) thienemanni Kieff.
O. (E.) rusticus ? Goetgh.
O. (Orthocladius) dentifer Brund.
O. (O.) frigidus (Zett.)
O. (O.) oblidens (Walk.)
O. (O.) rubicundus (Meig.)
O. (O.) rhyacobius (Kieff.)
O. (O.) saxicola (Kieff.)
O. (Pogonocladius) consobrinus (Holm.)
Orthosmittia albipennis (Goetgh.)
Paracladius conversus (Walk.)
Parakiefferiella bathophila (Kieff.)
P. coronata (Edw.)
Paralimnophyes hydrophilus (Goetgh.)
Parametriocnemus stylatus (Kieff.)
Paraphaenocladius impensus (Walk.)
P. irritus (Walk.)
P. pseudirritus Str.
Paratrichocladius rufiventris (Meig.)
P. skirwithensis (Edw.)
Paratrissocladius excerptus (Walk.)
Psectrocladius (Allopsectrocladius)
    obvius (Walk.)
P. (A.) platypus Edw.
P. (Mesopsectrocladius) barbatipes
    (Kieff.)
P. (Monopsectrocladius) calcaratus
    (Edw.)
P. (Psectrocladius) barbimanus Edw.
P. (P.) edwardsi Brund
P. (P.) fennicus Stora

P. (P.) psilopterus Kieff.
P. (P.) sordidellus (Zett.)
"Psectrocladius" turfaceus Kieff
*Pseudorthocladius curtistylus (Goetgh.)
P. filiformis (Kieff.)
Pseudosmittia trilobata (Edw.)
Rheocricotopus chalybeatus (Edw.)
*R. fuscipes (Kieff.)
*R. gouini (Goetgh.)
*Rheosmittia spinicornis Brund.
Smittia aterrima (Meig.)
S. contingens (Walk.)
S. edwardsi Goetgh.
*S. leucopogon (Meig.)
S. pratorum Goetgh.
Synorthocladius semivirens (Kieff.)
*Thalassosmittia thalassophila (Beq. and
    Goetgh.)
Thienimaniella acuticornis Kieff.
T. clavicornis Kieff
T. flavescens Edw.
T. majuscula Edw.
T. vittata Edw.
Tvetnia bavarica (Goetgh.)
T. clavescens (Edw.)
T. discoloripes (Goetgh.)
T. verralli (Edw.)
Zalutschia humphriesiae Dow. and Murr.

CHIRONOMINAE
    Chironomini
Chironomus (Camptochironomus) tentans
    Fabr.
Chironomus (Chironomus) annularius
    Auct.
C. (C.) anthracinus Zett.
C. (C.) aprilinus Meig.
C. (C.) cingulatus Meig.
C. (C.) dorsalis (Meig.) Auct.
*C. (C.) longistylus Goetgh.
C. (C.) lugubris Zett.
C. (C.) pilicornis Fabr.
C. (C.) plumosus (L.)
C. (C.) prasinus Meig.
C. (C.) pseudothummi Str.
C. (C.) riparius Kieff.
C. (C.) salinarius Kieff.
C. (C.) sp. A. (Pinder)
Cladopelma laccophila Kieff.

C. psittacinus (Meig.)
C. viridula (Fabr.)
Cryptochironomus lateralis (Goetgh.)
C. supplicans (Meig.)
Cryptotendipes pseudotener Goetgh.
Demeijerea rufipes (L.)
Demicryptochironomus vulneratus (Zett.)
Dicrotendipes lobiger (Kieff.)
D. nervosus (Staeg.)
D. notatus (Meig.)
D. pulsus (Walk.)
D. tritomus Kieff.
*Einfeldia longipes (Staeg.)
*E. pagana (Meig.)
Endochironomus albipennis (Meig.)
E. dispar (Meig.)
E. impar (Walk.)
E. tendens (Fabr.)
Glyptotendipes barbipes (Staeg.)
G. gripkoveni Kieff.
G. pallens (Meig.)
G. paripes Edw.
G. viridis Macq.
Graceus ambiguus Goetgh.
Harnischia falcata Kieff. (?)
*Kiefferulus tendipediformis Goetgh.
Lauterborniella agrayloides Kieff.
Microchironomus deribae Freem.
    (in helicopter fuel)
Microtendipes caledonicus Edw.
M. chloris Kieff.
*M. confinis (Meig.)
M. pedellus (deGeer)
M. rydalensis Edw.
M. tarsalis (Walk.)
Nilothauma brayi (Goetgh.)
Pagastiella orophila (Edw.)
Parachironomus arcuatus Goetgh.
P. frequens (Joh.)
P. monochromus (Wulp)
P. parilis (Walk.)
P. subalpinus Goetgh.
P. swammerdami Kreus.
P. tenuicaudatus (Mall.)
Paracladopelma laminata Kieff.
Paralauterborniella nigrohalteralis (Mall.)
Paratendipes albimanus (Meig.)
P. nudisquama (Edw.)
P. plebejus (Meig.)

Phaenopsectra (Phaenopsectra) flavipes
    (Meig.)
P. (P.) punctipes (Wied.)
P. (Sergentia) coracina (Zett.)
Polypedilum (Pentapedilum) nubens Edw.
P. (Pe.) sordens (Wulp)
P. (Pe.) tritum (Walk.)
P. (Polypedilum) acutum Kieff.
P. (P.) albicorne (Meig.)
P. (P.) arundinetum Goetgh.
P. (P.) convictum (Walk.)
*P. (P.) cultellatum Goetgh.
P. (P.) laetum (Meig.)
P. (P.) nubeculosum (Meig.)
P. (P.) pedestre (Meig.)
P. (Tripodura) bicrenatum Kieff
P. (T.) pullum (Zett.)
P. (T.) quadriguttatum Kieff.
P. (T.) scalaenum (Schr.)
Stenochironomus gibbus (Fabr.)
S. hibernicus Edw.
Stictochironomus histrio (Fabr.)
S. maculipennis (Meig.)
S. pictulus (Meig.)
S. rosenschoeldii (Zett.)
Xenochironomus xenolabis Kieff.
        Pseudochironomini
Pseudochironomus prasinatus (Staeg.)

        Tanytarsini
Cladotanytarsus atridorsum Kieff.
C. difficilis Brund.
C. mancus (Walk.)
*C. nigrovittatus (Goetgh.)
C. vanderwulpi Edw.
*Corynocera ambigua Zett.
*Microspectra apposita (Walk.)
M. atrofasciata (Kieff.)
M. bidentata Goetgh.
M. contracta Reiss
M. fusca (Meig.)
M. groenlandica And.
M. junci (Meig.)
*M. lindrothi Goetgh.
*M. notescens (Walk.)
M. recurvata Goetgh.
*Neozavrelia luteola Goetgh.
Parapsectra nana (Meig.)
*Paratanytarsus austriacus Kieff.

*P. bituberculatus (Edw.)
P. confusus Palmen
*P. dimorphis Reiss.
P. inopertus (Walk.)
P. intricatus Goetgh.
P. laccophilus Edw.
P. tenuis (Meig.)
*Rheotanytarsus distinctissimus (Brund.)
R. pentapoda Kieff.
Stempellina bausi (Kieff.)
Stempellinella brevis Edw.
Tanytarsus bathophilus (Kieff.)
*T. brundini LInd.
T. buchonius Reiss and Fittkau
*T. curticornis Kieff.

*T. debilis (Meig.)
T. eminulus Walk.
T. glabrescens Edw.
*T. gracilentus Holmgr.
T. gregarius (Kieff.)
T. lestagei (aggregate)
T. medius Reiss and Fittkau
T. pallidicornis Walk.
T. quadridentatus Brund.
T. signatus Wulp
*T. striatulus Lindeberg.
*T. sylvaticus Wulp
T. usmaensis Pag.
Virgatanytarsus arduennensis (Goetgh.)
V. triangularis (Goetgh.)

TABLE 2.   The occurrence of chironomid genera in Ireland, Britain and mainland Europe. Numbers of species recorded to date in Ireland given in brackets ( ).

	IRELAND		BRITAIN	EUROPE
Tanypodinae	24	(55)	24	27
Podonominae	1	(1)	2	5
Telmatogetoninae	1	(1)	2	3
Buchonomyiinae	1	(1)	1	1
Diamesinae	4	(13)	6	11
Prodiamesinae	2	(3)	3	3
Orthocladiinae	52	(134)	52	70
Chironominae	43	(139)	43	66
TOTAL	128	(347)	133	186

TABLE 3. The known occurrence of genera and species of the Chironomidae and species of the Ephemeroptera and Trichoptera in Ireland, Britain and mainland Europe.

	IRELAND	BRITAIN	EUROPE
CHIRONOMIDAE			
Genera	128	133	186
%Europe	69%	71%	100%
%Britain	92%	100%	—
Species	347	460	1200
%Europe	29%	38%	100%
%Britain	70%	100%	—
EPHEMEROPTERA			
Species	29	47	217
%Europe	13%	21%	100%
%Britain	62%	100%	—
TRICHOPTERA			
Species	144	197	895
%Europe	16%	22%	100%
%Britain	73%	100%	—

Male Dimorphism in an Arctic Chironomid
(Diptera: Chironomidae)

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ABSTRACT. — *Oliveridia tricornis* (Oliver) has two male morphs differing primarily in antennal structure. The long-antennal morph has 13 flagellomeres and the short-antennal morph has female-like antennae with 5-7 flagellomeres. No differences in depth or substrate preference of the larvae, nor seasonal emergence or behaviour of adults were found. The morphs occur in a ratio of 3 short-antennal morphs: 1 long-antennal morph.

INTRODUCTION

A number of male arctic chironomids are known to have structural modifications such as reduced antennae and wings, strengthened legs, and enlarged hypopygia (Downes 1962; Oliver 1976; Danks 1981). Usually all males of a species share these structural modifications with little or no variation between individuals. But male dimorphism apparently exists in at least two species, *Oliveridia tricornis* (Oliver 1976) and *Hydrobaenus fusistylus* Saether (1976). In *O. tricornis* the two morphs differ primarily in antennal structure. Although Oliver (1976) regarded the two morphs as belonging to the same species, the possibility that they belonged to two sympatric, sibling species was conceded. This paper is a contribution towards resolving the problem of whether or not male dimorphism exists in *Oliveridia tricornis*.

Information on the taxonomy, ecology and life history of *O. tricornis* can be found in Welch (1973, 1976) and Oliver (1976). No comparable dimorphism has been found in females or immature stages. The larvae inhabit small to large oligotrophic to ultra-oligotrophic lakes. They prefer silt substrates, either in areas of pure silt or in rocky areas with the spaces between the rocks filled with silt. Larval development takes two years. Emergence begins soon after ice-off or in late seasons during the period of ice-off. Adults rarely swarm but congregate for mating on lake shores or on the ice. The males exhibit some of the structural modifications generally associated with loss of the habit of mating in swarms (Brundin 1966; Downes 1969; Hansen and Cook 1976; Oliver 1981). The antennal plume is

235
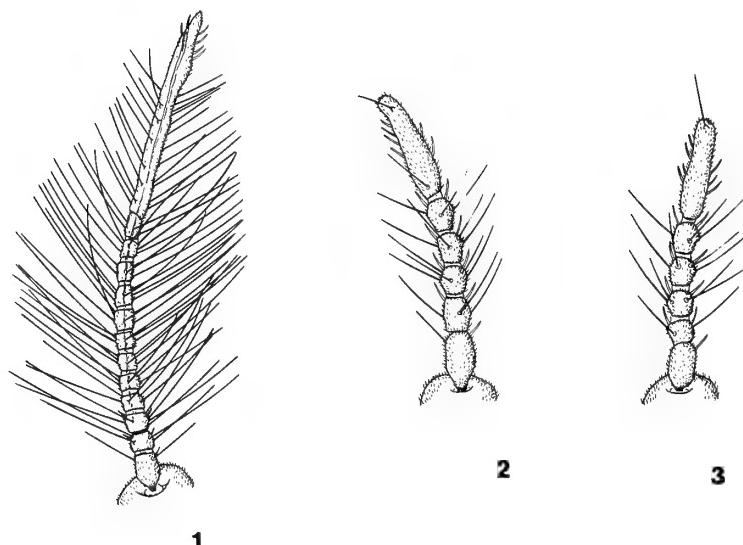
FIGS. 1-3.   *Oliveridia tricornis* (Oliver). Antennae: 1. Male, long-antennal morph; 2. Male, short-antennal morph; 3. Female.

reduced in both morphs, the legs are somewhat elongated and strengthened, and the hypopygium is enlarged and elaborated.

MATERIALS AND METHODS

In 1971 and 1972, Dr. H.E. Welch carried out an intensive trapping program of chironomids emerging from Char Lake (74°12′ N, 95°53′ W), Cornwallis Island, N.W.T., Canada (Welch 1973). In 1971, submerged emergence traps were laid out along transects radiating from shallow to deep areas of the lake (see Fig. 1 in Welch 1973). Along transects A and C the traps were set over 1, 2, 3, 4, 6, 8, 10, 16, 19, 22, and 23m depths. They were emptied every three days after solar noon.

The emergence trap specimens from 1971 were analyzed to determine if differences in depth distribution or pattern or annual emergence existed between the two morphs. There was no essential difference in results from the various transects. Therefore only the results from transect C are presented herein.

ANTENNAL ANATOMY

The antenna of the long-antennal morph (Fig. 1) has 13 flagellomeres, sensilla chaetica on flagellomeres 1-3 and 13, and no subapical seta. The

Fɪɢ. 4. *Oliveridia tricornis* (Oliver). Head with both long and short antennae, frontal view.

plume is partly reduced and the extent of reduction varies between individuals. That of the short-antennal morph (Fig. 2) has 5-7, usually 6, flagellomeres, sensilla chaetica on each flagellomere, and a strong subapical seta. It is female-like (cf. Fig. 3) including the setal arrangement and absence of an antennal groove.

Several thousand specimens from Char Lake and elsewhere in the North American arctic have been examined and no intermediates between the antennae of the two morphs have been found. However, among the emergence trap specimens from Char Lake, three specimens had both types of antennae (Fig. 4). The long antenna was present on the left side of the head in two of the specimens and on the right side of the third.

Depth Distribution

The total number of each morph emerging from various depths along transect C is presented in Fig. 5. Emergence patterns and numbers of specimens were similar between transects A and C (compare Fig. 5 with Fig. 6 of Welch 1973).

Numbers of short-antennal morphs emerging outnumbered those of the long-antennal morphs by about three to one. Both morphs emerged from all depths sampled, and in the same pattern. Emergence peaked at 2-4m (rock-silt zone) and decreased at 4-8m (moss zone). It peaked again at 10m (silt zone) and steadily decreased from 10-25, the maximum depth sampled.

Annual Emergence

The annual emergence of each morph is presented in Fig. 6. The short-antennal morph outnumbered the long-antennal morph by about 3:1 but there was no difference in the pattern of annual emergence. There was also
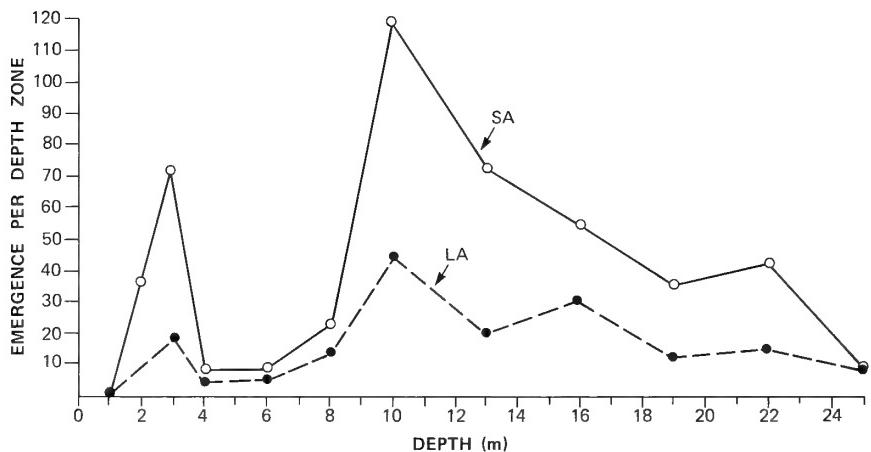
FIG. 5.   Comparison of total emergence of long-antennal morphs (LA) and short-antennal morphs (SA) against depth.
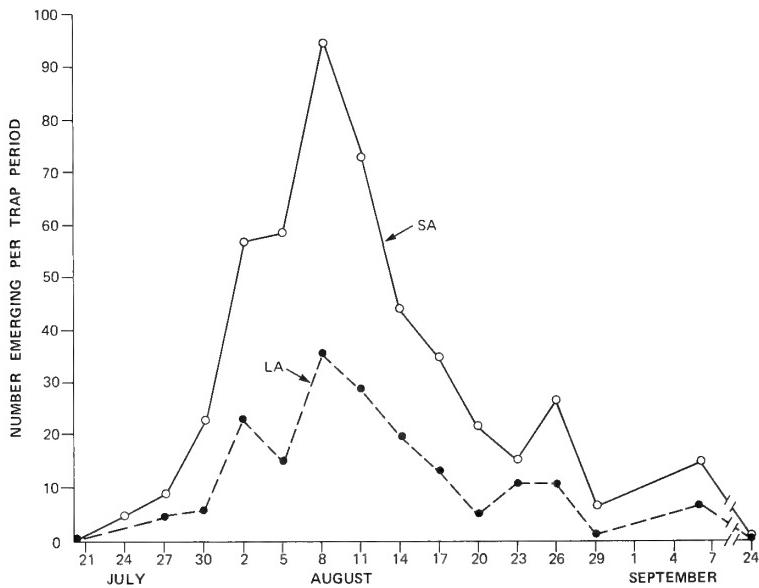
FIG. 6.   Comparison of annual emergence of long-antennal morphs (LA) and short-antennal morphs (SA).

no difference in the total duration of emergence between the two morphs as the onset and termination of emergence is the same. Cumulative emergence curves (Fig. 7) emphasize the similarity of annual emergence patterns. As in
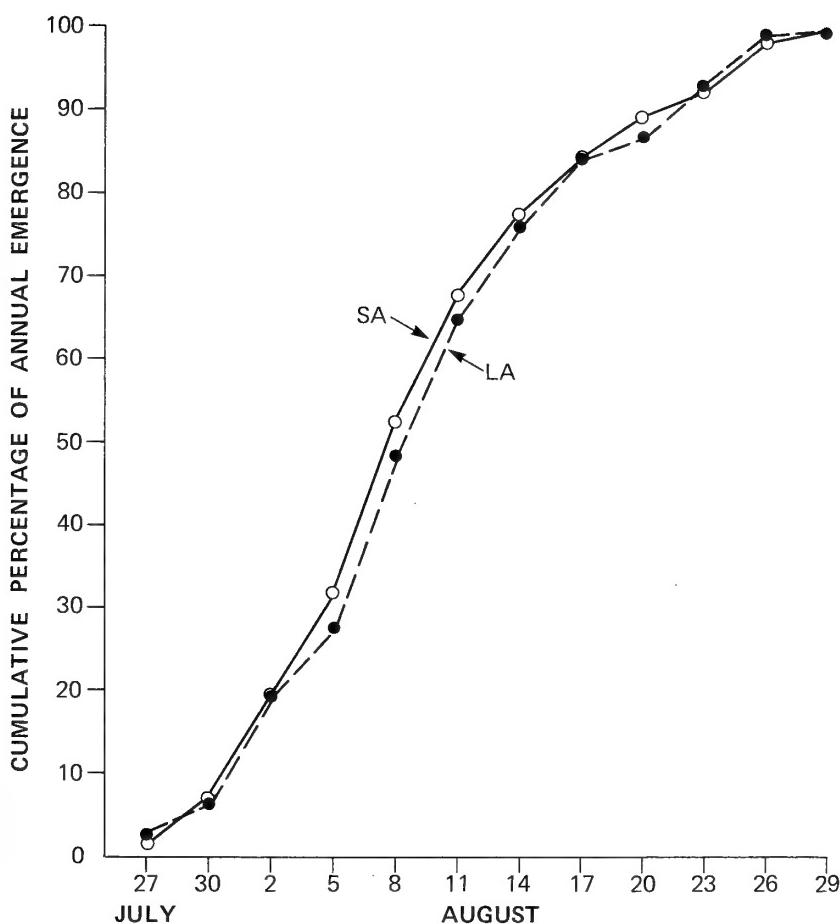
Fig. 7.   Comparison of cumulative emergence of long-antennal morphs (LA) and short-antennal morphs (SA).

other arctic chironomids, emergence is highly synchronized (Danks and Oliver 1972; Welch 1973), with emergence of both morphs attaining 50% of the annual total at the same time.

DISCUSSION

The long-antennal and short-antennal morphs of *O. tricornis* emerged simultaneously from various depths throughout the emergence period. No depth or substrate preference was exhibited between the larvae of the two morphs. The adults congregated in the same areas and mated on substrate.

No difference in mating behaviour was observed (Oliver 1976; pers. obs.). The two morphs participated in the rarely occurring swarms (Oliver 1976). Thus, there is no evidence that reproductive isolation exists between the two morphs. To the contrary, all ecological and life history data strongly indicated that there is ample opportunity for exchange of genetic material between the two morphs and it is concluded that they belong to the same species.

The 3:1 ratio of short-antennal morphs is not restricted to Char Lake in the Nearctic. The two morphs consistently were collected together in a 3:1 ratio in other areas of the Nearctic (Oliver 1976; pers. obs.). The short-antennal morph is dominant in the Nearctic but it has not been collected in Spitzbergen (Oliver 1976; Saether pers. comm.). This suggests that the short-antennal morph, undoubtedly the more derived form, has originated in the Nearctic or at least in Beringia.

REFERENCES

BRUNDIN, L.   1966.   Transantarctic relationships and their significance as evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. K. svenska Vetenska-Acad. Handl. 11:1-472.

DANKS, H.V.   1981.   Arctic Arthopods. A review of systematics and ecology with particular reference to the North American fauna. Ent. Soc. Can., Ottawa. 608 pp.

DANKS, H.V. AND D.R. OLIVER.   1972.   Seasonal emergence of some high arctic Chironomidae (Diptera). Can. Ent. 104:661-686.

DOWNES, J.A.   1962.   What is an arctic insect? Can. Ent. 94:143-162.

————————.   1969.   The swarming and mating behaviour of Diptera. A Rev. Ent. 14:271-298.

HANSEN, D.C. AND E.F. COOK.   1976.   The systematics and morphology of the Nearctic species of *Diamesa* Meigen, 1835 (Diptera: Chironomidae). Mem. Amer. Ent. Soc. 30:1-203.

OLIVER, D.R.   1976.   Chironomidae (Diptera) of Char Lake, Cornwallis Island. N.W.T., with descriptions of two new species. Can. Ent. 108:1053-1064.

————————.   1981.   Redescription and systematic placement of *Oreadomyia albertae* Kevan and Cutten-Ali-Khan (Diptera: Chironomidae). Quaest. Entomol. 17:121-128.

SAETHER, O.A.   1976.   Revision of *Hydrobaenus, Trissocladius, Zalutschia, Paratrissocladius,* and some related genera (Diptera: Chironomidae). Bull. Fish. Res. Bd. Can. 195:1-287.

WELCH, H.E.   1973.   Emergence of Chironomidae (Diptera) from Char Lake, Resolute, Northwest Territories. Can. J. Zool. 51:1113-1123.

————————.   1976.   Ecology of Chironomidae (Diptera) in a Polar Lake. J. Fish. Res. Bd. Can. 33:227-247.

A Field Method to Quantitatively Sample Sand Invertebrates

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Abstract. — The use of CO_2 flotation was found to be 89-95.6% effective in separating invertebrates from sand samples. It can be used under field conditions to obtain samples of living material and to make quantitative estimates of sand populations. For quantitative work, two fresh CO_2 rinses are necessary. The paper also gives preliminary estimates of populations of Chironomidae in the clean sand of the Blackwater River, Florida.

Many streams in northern Florida, particularly the acid streams, have a unique benthos associated with sand substrates. One of these is the Blackwater River, an undisturbed, protected, sand-bottom river in the Blackwater River State Forest, Okaloosa and Santa Rosa Counties, Florida. Many studies on sand substrates have been restricted by a lack of precise methods for separating the fauna from the sand, but there are two studies that provide quantitative estimates of the Blackwater River sand fauna (Bass & Hitt 1977, Tsui & Hubbard 1979).

Separating the fauna from the sand either with sieves or by hand has presented problems. Invertebrates, particularly small ones, are probably missed in both processes, and hand-sorting is too tedious and time-consuming for general use. Other separation methods include flotation (soap, oil, sugar, CO_2), elutriation, and centrifugation (Edmondson & Winberg 1971). Centrifugation requires that samples be sorted with a centrifuge in the laboratory, limiting its use in the field. We tried the other methods at least once under field conditions in an effort to find a method that separated live invertebrates from sand with relative ease and accuracy. Flotation with CO_2 offered the greatest promise and this paper gives results of experiments designed to find the most efficient way of using CO_2 to float live invertebrates from the clean sand.

Methods

Studies were made in the clean sand of the Blackwater River, Okaloosa Co., Florida, which was described by Beck (1973), Peters and Jones (1973),

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Bass and Hitt (1977), and Peters and Peters (1977). Sand analysis showed that 75-90% of sand by weight was in the size categories from 0.25-1.00 mm diameter ($\varnothing$1,2) with less than 0.5% very fine sand and silt (≤ 0.125 mm diameter). Changes in the relative proportions of $\varnothing$1 and $\varnothing$2 occurred with changes in current. Experiments were conducted on 26-IV, 2-V, and 9-V-1981 in water 36 to 68 cm deep with a current of 45 to 60 cm/sec and temperatures of 21.2 to 23.5°C.

Circular samplers of three standard lengths (5 cm, 10 cm, 15 cm) and various widths retrieved approximately 100 cm^3 of sand per sample. A corer of PVC pipe was used to sample depths greater than 15 cm. Since compactness of the sand varied and some of each sample was lost during retrieval, actual sand volume was measured for each sample so that the number of animals per unit volume of sand could be determined with precision.

Each sample was placed in a 0.35 litre jar. The jar was filled with water saturated with CO_2, corked, agitated 10-30 sec, and the elutriate decanted over filter paper. At first, we used bottles of club soda as a source of CO_2, but later changed to a soda water bottle with CO_2 gas canisters. For experiments, the filter paper, the sample, and the sand were stained with a solution of 1% rose bengal and preserved in 10% formalin. Formalin was used to keep oligochaetes intact until counted and this was fairly successful. We then counted all specimens floated by the CO_2 and all specimens left in the sand under a microscope. Each taxon in a sample was treated as an individual trial. Only trials containing more than 10 specimens were included in Table 3.

RESULTS

Experiments with a single CO_2 rinse collected only 59.8 ± 20.8% of invertebrates present (13 trials, range 26.7-94.0%), a result too low and too variable for quantitative work. Results for two samples with four rinses, recharging the CO_2 before the first and third rinse, are given in Table 1 (data pooled for all groups except Chironomidae). Most animals were collected only after the freshly charged first and third rinses, suggesting that a fresh CO_2 charge was necessary. Table 2 gives total data for a single core using three fresh CO_2 rinses. Although Chironomidae were underrepresented, it was these data that influenced the choice of two CO_2 rinses since a third rinse only contributed about 5% to the total numbers. Subsequent samples used two fresh CO_2 rinses. Two CO_2 rinses, both freshly charged, will give overall estimates of better than 90% of populations present (Table 3). In the Chironomidae, an average 95.6% of the population was estimated (range 89.3-100%).

	N	Number of rinses			
		1	2	3	4
Chironomidae	67	65.7	74.6	95.5	97.0
	27	70.4	77.8	88.9	92.6
Other benthos	230	56.5	65.2	90.9	91.3

TABLE 1. Percentage of invertebrates collected after four consecutive rinses with CO_2 recharged before first and third rinse.

Depth into sand	Volume (cm^3)	Taxon	Number/rinse			N in sand	Total
			1	2	3		
0.0– 4.7 cm	60	CH	2	2	0	0	4
		EN	9	6	1	1	17
		NE	3	2	0	0	5
		CO	0	1	0	0	1
4.7– 10.1 cm	70	CH	1	3	0	0	4
		EN	34	17	3	4	58
		NE	6	1	1	0	8
		CO	11	0	2	1	14
10.1– 15.7 cm	72	EN	15	20	2	1	38
		NE	1	1	0	0	2
		CO	4	10	1	0	15
15.7– 20.7 cm	64	EN	30	4	1	0	35
		NE	4	0	0	0	4
		CO	78	1	4	0	83
	266		198	68	15	7	288

TABLE 2. Numbers of invertebrates collected in a single core (2V-1981, water depth of 55 cm) treated with three rinses. CO_2 was recharged before each rinse. Abbreviations: CH, Chironomidae; EN, Enchytraeidae; NE, Nematoda; CO, Copepoda.

Taxon	Trials	N collected	N present	Average % /trial
Chironomidae	6	424	436	95.6 ± 4.0
Enchytraeidae	10	910	1016	90.7 ± 3.6
Nematoda	6	363	374	95.2 ± 5.5
Copepoda	3	104	112	89.0 ± 9.1
	25	1801	1938	92.7 ± 5.3

TABLE 3. Percentages of invertebrates collected after two rinses with CO_2 recharged before each rinse.

Few of the invertebrates living in the sand can be identified with any degree of certainty. Some of the Copepoda belong to the harpacticoid genus *Parastenocaris* (based on Pennak 1978). Although they have been sent to specialists, the Nematoda are not yet identified. A single species of Enchytraeidae, *Barbidrilus paucisetus* Loden & Locy, represents the oligochaetes in clean sand. The Chironomidae, identified from larvae or pupae, belong to the Orthocladiinae (*Lopescladius* Oliveira, *Rheosmittia* Brundin, *Corynoneura* Winnertz, *Thienemanniella* Kieffer) and the *Harnischia* group of Chironomini [*Robackia claviger* (Townes), "*Cryptochironomus*" sp. Pagast, *Demicryptochironomus* Lenz]. Additional genera and species of Chironomidae are likely to be found in sand samples from other dates and habitats.

DISCUSSION

The CO_2 flotation method was efficient in clean sand substrates and apparently anesthetized and bubbled out invertebrates present in the sand; individuals returned directly to fresh water remained alive. It was also effective in fine gravel/sand (unpublished data). The method was unsuccessful in silt habitats because silt was bubbled off with the fauna.

We sampled Chironomidae in different sand habitats of the Blackwater and our results using CO_2 flotation can be compared with those of two published reports. For comparison, we have converted all results to numbers/m^2 to a depth of 10 cm into the sand. Bass and Hitt (1977)

Body length	1,2-III-1981*		9,12-V-1981**	
	N	%	N	%
≥ 6 mm	3	.4	5	.3
< 6mm > 1 mm	321	37.5	201	12.7
≤ 1 mm	532	62.1	1372	87.0

* 28 samples totaling 1998 cm^3 sand.
** 26 samples totaling 2315 cm^3 sand.

TABLE 4. Size groupings of Chironomidae collected from sand habitats in the Blackwater River, Florida.

surveyed the fauna of the Blackwater using an Ekman dredge and sieves. Their samples taken "near-shore" and "mid-river" averaged 31 (2-II-1977) and 113 (9-V-1977) chironomids/m^2. Tsui and Hubbard (1979) hand-sorted litre samples of sand which had been taken from random depths and preserved in formalin stained with rose bengal. These samples averaged 6,500-9,000 chironomids/m^2 (II, III, IV-1974). Our averages were 53,744 (1,2-III-1981) and 75,723 (9,12-V-1981). These averages were calculated from totals for three 10 cm samples each at depths of 38 to 45 cm (current 44 to 45 cm/sec) and 60 to 72 cm (current 60 to 62 cm/sec). Mean numbers/cm^3 for the two habitats were respectively: March, .846 ± .102 and .153 ± .058; May, 1.044 ± .118 and .469 ± .211.

The differences between our data and those of Bass and Hitt (1977) demonstrate that dredge and sieve methods underestimate populations of sand chironomids. Sieves cannot adequately separate sand particles from midges when both are of similar size, and Flannagan (1970) showed that the Ekman dredge is not reliable in sand. Only when all chironomids less than 6 mm in body length (Table 4) are excluded from our data do the CO_2 flotation estimates compare with the dredge and sieve estimates.

Table 4 gives totals for all Chironomidae collected from samples 2 cm to 27 cm into the sand. These data give a rough estimate of the size distribution of chironomids: most were larvae of 1 mm body length or less (Table 4). Quantitative estimates based only on the percentage of larvae greater than 1 mm body length would approximate the figures given by Tsui and Hubbard (1979). However, the samples of Tsui and Hubbard were taken in a different year when the river was 15 to 58 cm deeper, so differences in estimates of chironomid populations may represent annual population fluctuations or a broadened dispersal. The increased substrate available with a

wider stream bed compensates for an apparent reduction in species density, as was shown for mayflies by Lehmkuhl and Anderson (1972).

We do suspect that hand-sorting large samples of sand overlooks many chironomids less than 1 mm in body length. In using hand-sorting to evaluate invertebrates left in the sand (Tables 1-3), we used small samples sorted with care under a microscope, and it seems that the small midges were the first to be floated off by CO_2; however, some may have been missed since every sand grain was not individually examined. If so, overall efficiency may be somewhat less than calculated in Table 3. Whether or not hand-sorting is as accurate as CO_2 flotation, the use of CO_2 has other advantages: sorting time is reduced; small larvae are easily retrieved; and live material is collected.

Acknowledgments

Literature Cited

BASS, D.G., JR. AND V.G. HITT. 1977. Ecology of the Blackwater River system, Florida. Northwest Streams Res. Proj., Florida Game & Freshw. Fish Comm.

BECK, W.M., JR. 1973. Chemical and physical aspects of the Blackwater River in Northwestern Florida. *In:* Peters, W.L. & J.G. Peters (eds.), Proc. 1st Int. Conf. Ephemeroptera. E.J. Brill, Leiden. p. 231-239.

EDMONDSON, W.T. AND G.G. WINBERG (eds). 1971. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters (IBP Handbook No. 17). Blackwell Sci. Publ., Oxford.

FLANNAGAN, J.F. 1970. Efficiencies of various grabs and corers in sampling freshwater benthos. J. Fish. Res. Board Can. 27:1691-1700.

LEHMKUHL, D.M. AND N.H. ANDERSON. 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology 53:661-667.

PENNAK, R.W. 1978. Freshwater Invertebrates of the United States. 2nd ed. Wiley Interscience, New York.

PETERS, W.L. AND J. JONES. 1973. Historical and biological aspects of the Blackwater River in Northwestern Florida. *In:* Peters, W.L. & J.G. Peters (eds.), Proc. 1st Int. Conf. Ephemeroptera. E.J. Brill, Leiden. p. 242-251.

_____ AND J.G. PETERS. 1977. Adult life and emergence of *Dolania americana* in Northwestern Florida (Ephemeroptera: Behningiidae). Int. Rev. Gesamten Hydrobiol. 62:409-438.

TSUI, P.T.P. AND M.D. HUBBARD. 1979. Feeding habits of the predaceous nymphs of *Dolania americana* in Northwestern Florida (Ephemeroptera: Behningiidae). Hydrobiologia 67:119-123.

Observations on the Life-cycles of some Chironomidae in Southern England

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Abstract. — The life-cycles of 10 species of chironomid inhabiting the bottom sediments of a stream in southern England are described. The number of generations per year ranged from 1 to 5, but the pattern for several species differed between the 2 years under discussion, thus illustrating the difficulty of interpreting insect life-cycles from observations made at a single site over a restricted period of time, as is usually the case.

Introduction

Despite the wealth of literature dealing with various aspects of the ecology of the Chironomidae (Fittkau, Reiss & Hoffrichter, 1976; Hoffrichter & Reiss, 1981), the life-cycles of very few species have been elucidated and this is especially the case in relation to riverine species.

The observations on which this paper is based were made on a 100 m reach of the Tadnoll Brook, a small chalk-stream in southern England, previously described by Pinder (1974).

Chalk streams derive the bulk of their flow from springs emanating from the chalk aquifer. As a result, they are characterized by having relatively stable flow and temperature regimes. In the south of England, chalk springwater has a more or less constant temperature of 10°C-11°C which has the effect of making the rivers it feeds relatively warm in winter and cool in summer. January is typically the coldest month with a mean river-water temperature of about 6°C and July is the warmest with a mean of about 15°C. Discharge follows a seasonal pattern with peak flows in late autumn and winter, decreasing to a minimum in late summer. Violent floods are rare. The physical, chemical and biological characteristics of southern English chalk-streams are described by Ladle and Casey (1979).

The Study Site

Although more or less a typical chalk-stream in terms of its chemistry, the study reach of the Tadnoll Brook differs from most chalk-streams in that its

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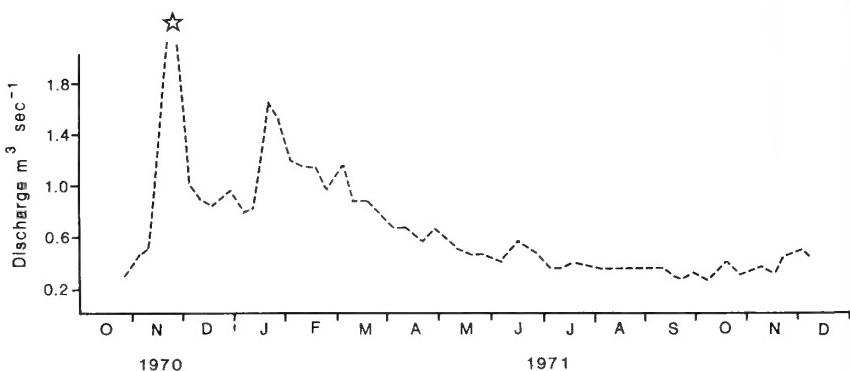
FIG. 1.   Discharge recorded a short distance upstream of the sampling site. (Asterisk indicates that stream was over its banks.)

bed is mainly composed of sand and organic detritus rather than gravel. The detritus deposits, which are mostly to be found in slack marginal areas and in the lee of weedbeds, develop during summer and early autum when discharge is low and are dispersed by the first floods which usually occur in autumn.

Discharge data are available for most of the period under consideration (Fig. 1), and show that flow-rate was high during most of the autumn and winter of 1970, but remained low for the whole of 1971.

Temperature data are only available for 1971 (Table 1) but data from other nearby rivers suggest that water temperatures in 1970 were little different.

SAMPLING METHODS

Samples were obtained at roughly 2 week intervals between March 1970 and the end of 1971. On each sampling occasion, 30 cores, each 55 mm in diameter, were taken at random from within a 100 m reach of stream, which at this point is 4 m to 5 m wide with a depth in summer of between 0.5 m

TABLE 1.   Monthly mean water temperatures at the study site during 1971.

JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEPT	OCT	NOV	DEC
5.6	5.7	7.9	9.0	10.5	12.3	15.7	14.4	12.3	10.9	6.7	6.6

and 1.5 m. The depth to which the corer was inserted into the substratum varied according to the nature of the sediment, but was at least 200 mm. Preliminary sampling had indicated that very few larvae occurred below 100 mm.

Samples were washed through a sieve of 125 μm aperture, sorted under $10\times$ magnification and mounted in dimethyl hydantoin formaldehyde (DMHF) resin for subsequent identification and measurement.

RESULTS

Despite using a relatively fine sieve (125 μm), very few first instar larvae were found. Undoubtedly first, and to a lesser extent second, instar larvae are capable of passing through such a sieve with ease. In presenting the data for individual species estimates of total population density are shown (Fig. 2-11) together with the proportion of fourth instar larvae.

Logarithmic, 95% confidence intervals were calculated from the data and in general fell within about 30% of the mean, at least when population size was reasonably large. However, in the interpretation of life-cycles, it is the trends in population size and changes in the proportions of age classes which are of interest, rather than statistically significant differences between particular samples.

Subfamily TANYPODINAE

Apsectrotanypus trifascipennis (Zett.)   Fig. 2

This was the most abundant species of the subfamily with a peak population density approaching 2000 m^{-2} in November 1971. However, the majority of larvae occurred in association with deposits of organic detritus (Pinder 1980), especially coarse material of allochthonous origin so that local densities were much greater.

The decline in the number of larvae following autumn floods is well shown by the 1970 data, whereas in 1971 when discharge remained low, no such dramatic decline occurred.

The small number of larvae present in the early part of the year makes interpretation of this part of the life-cycle very difficult. In both years, the main recruitment occurred from August onwards with evidence of 2 influxes of young larvae in August/September and October/November.

Lindegaard-Petersen (1972) found pupae of this species in Linding Å during May and June and from August to September. Ringe (1974) recorded a small number of adults emerging from the Breitenbach in May and a main emergence period extending from July to September. In the present study, a
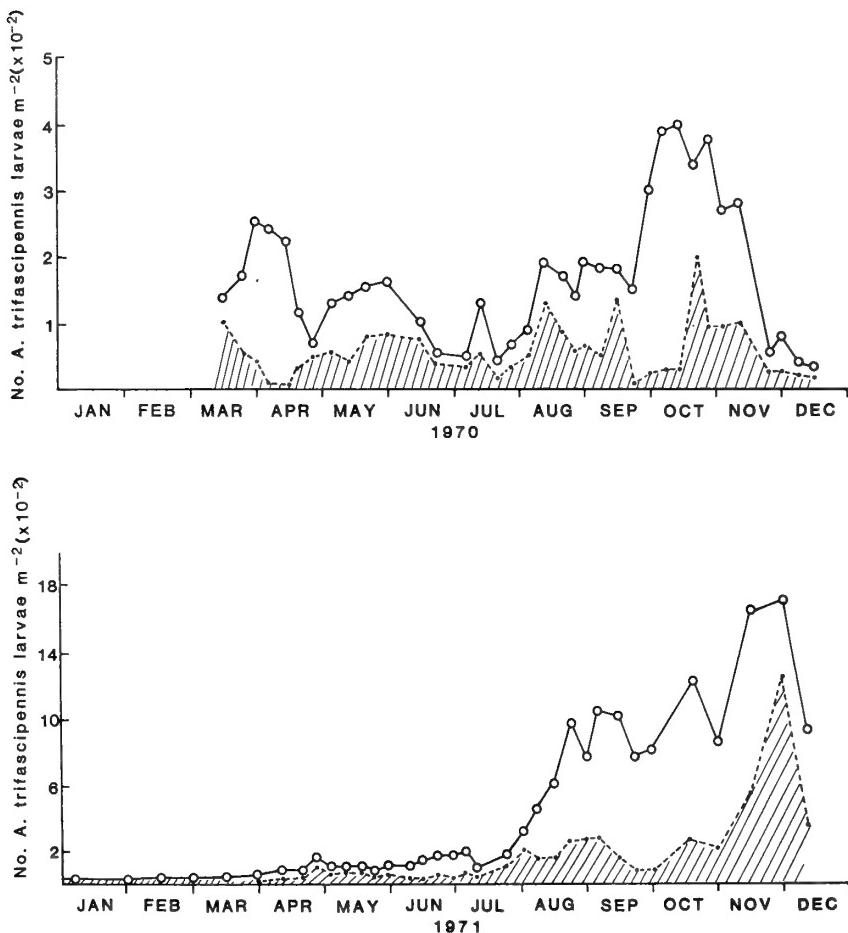
Fig. 2.   Population density of *A. trifascipennis*. Solid line = all larvae, broken line = fourth instar only.

few pupae were taken in May 1970 and pupae occasionally occurred in samples during July, August and September of both years.

Thus, the life-cycle appears to be similar in each of these 3 rivers with an overwintering population emerging in late spring. In the Tadnoll Brook, overwintering occurred as third and fourth instar larvae. A small summer generation apparently emerged during July and 2 overlapping generations during late summer resulted in a rapid increase in population density. The
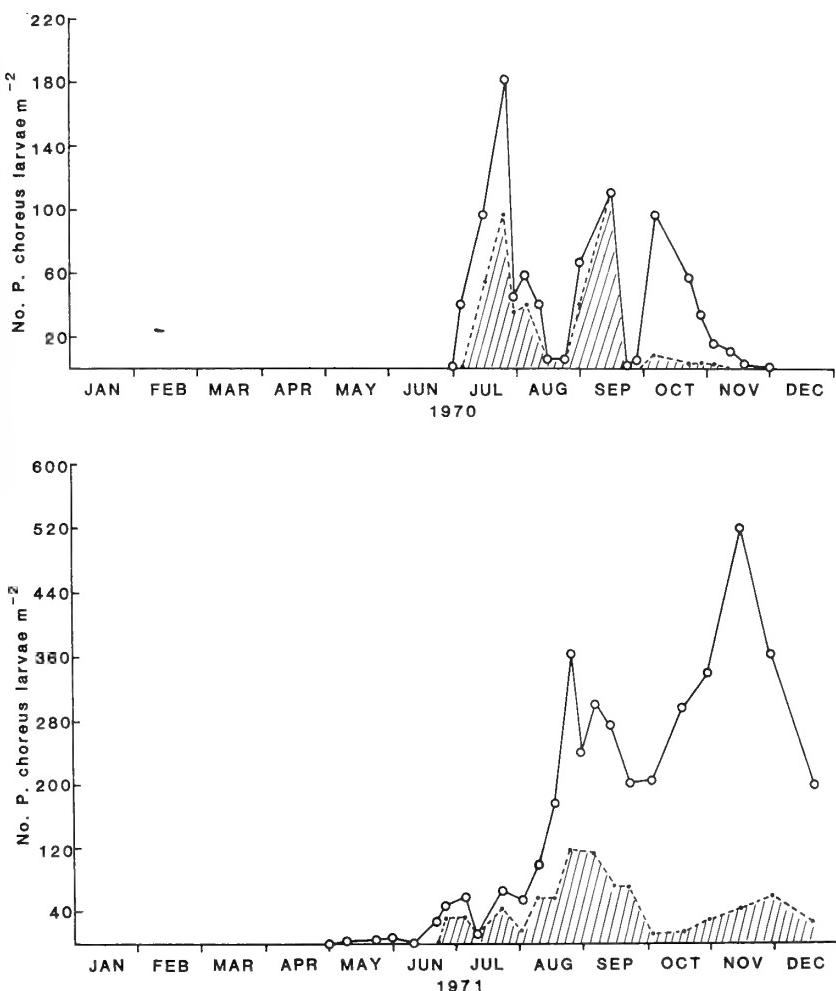
FIG. 3.   Population density of *P. choreus*. Solid line = all larvae, broken line = fourth in-star only.

second of these produced the overwintering population, the success of which was largely dependent on the extent to which beds of organic detritus were disrupted by autumn and winter spates.

Procladius choreus (Meigen)   Fig. 3

Apart from *A. trifascipennis,* this was the only tanypodine to occur in reasonably large numbers in samples. Trends in population density were

similar to those of *A. trifascipennis* and the 2 species occupied apparently similar niches.

In 1970, no larvae of *P. choreus* were found until the end of June. Thereafter, 3 well-defined generations were evident in July/August, August/September and October/November. During the last of these generations, almost all larvae in samples were second instars and the population declined to zero by the end of November, well in advance of the first autumn floods.

Larvae did not reappear in samples until May of 1971. Thereafter there was some evidence of a small generation emerging early in July and 2 major periods of recruitment in August/September and October/November. As in the previous year, the great majority of larvae from October onwards were second instars and although numbers declined from early November, a reasonable population persisted to the end of the year.

Although there was no sign of an overwintering population at this site in either of the preceding years, it is probable that the very small number of larvae (all 4th instar) which were found in May 1971 represented the residue of an overwintered population which entered the study reach by immigration from upstream.

If this interpretation is correct, the life-cycle consists of an overwintering generation emerging in April/May and 2 summer generations. Ford (1957) came to a similar conclusion regarding the timing of the overwintering generation, but detected only 1 protracted summer generation, probably because he sampled at monthly intervals.

SUBFAMILY DIAMESINAE

Potthastia gaedii (Meigen)   Fig. 4

In 1970, numbers of this species were low, with evidence of 2 distinct generations, in spring and late summer respectively. In 1971, when numbers were much greater, the pattern of generations was much more difficult to discern.

No indication of an overwintering population was found until the beginning of March 1971 when low numbers of third and fourth instar larvae began to appear in samples and persisted until the beginning of May. The timing of this agrees with that of the first apparent generation of 1970 when numbers were much greater. A clearly defined generation occurred in early summer, emerging in the second half of June. After a short break, larvae reappeared and thereafter were present to the end of the year. From July onwards, the data indicate at least 3 periods of recruitment: in July, late August to early September and October/November, with small numbers of
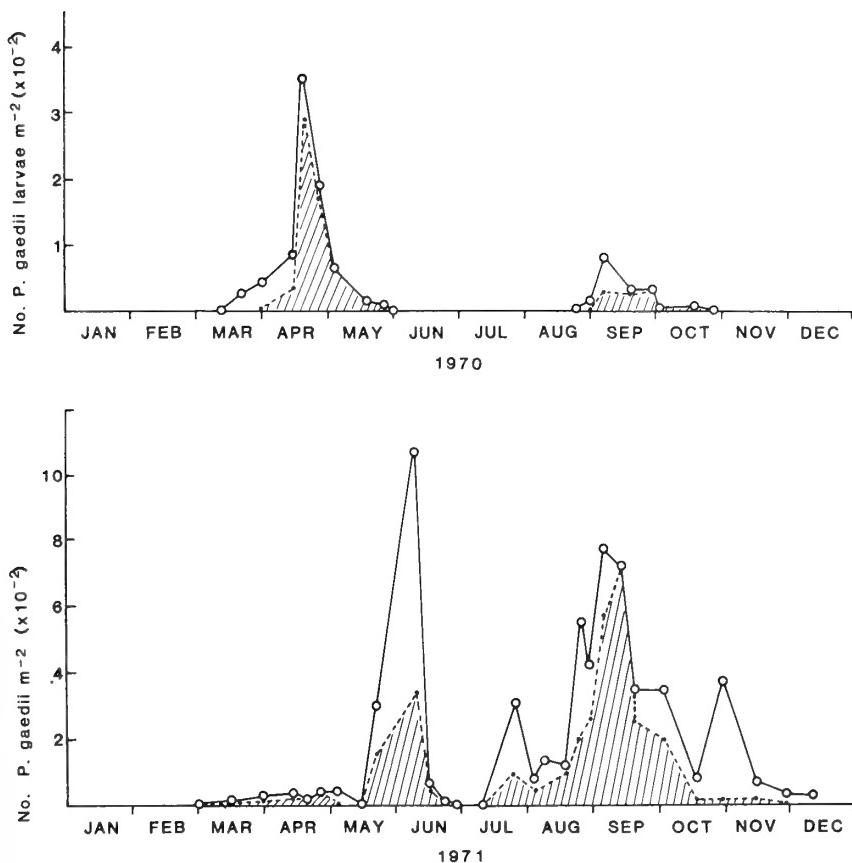
FIG. 4.   Population density of *P. gaedii*. Solid line = all larvae, broken line = fourth instar only.

second and third instar larvae persisting to the end of the sampling period. *P. gaedii* thus had 4 generations at the study site during 1971.

SUBFAMILY PRODIAMESINAE

Prodiamesa olivacea (Meigen)   Fig. 5

Third and fourth instar larvae of this species first occurred in samples in late May 1970 and by mid-July virtually all had developed to fourth instar. Numbers declined from July onwards and by the latter half of September were absent, reappearing in October and overwintering, largely as fourth in-
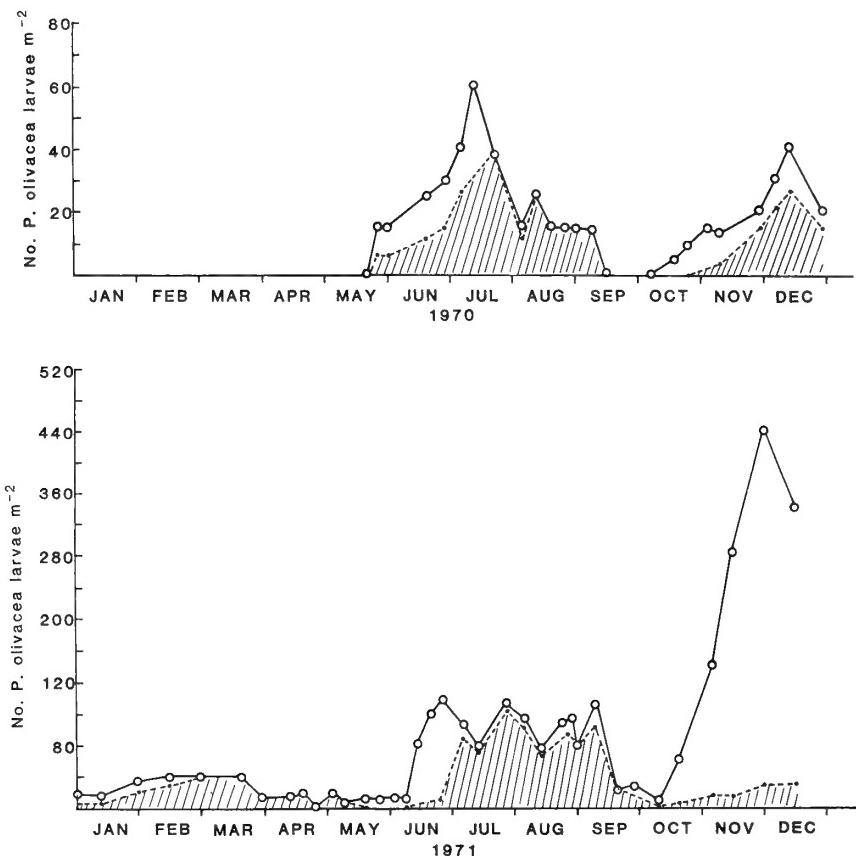
FIG. 5.   Population density of *P. olivacea*. Solid line = all larvae, broken line = fourth instar only.

star larvae from which adults emerged in early spring. Subsequent trends in 1971 were similar to those of the previous year except that the overwintering population, to the end of December, consisted principally of second and third instar larvae.

P. olivacea thus has 2 annual generations in the Tadnoll Brook, with summer development being slow by comparison with the other species considered. Pinder (1974) found adults on sticky-traps during July, August and September, indicating a protracted emergence period.

Ford (1957) also noted a similar timing for the overwintering generation but failed to demonstrate adequately the occurrence of a summer generation.
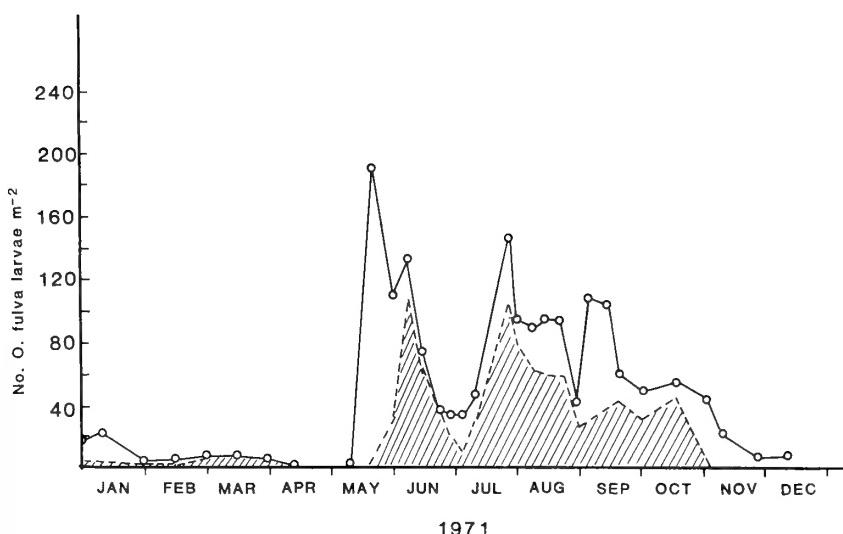
Fig. 6. Population density of *O. fulva*. Solid line = all larvae, broken line = fourth instar only.

Odontomesa fulva (Kieffer)   Fig. 6

Except for very occasional second instar larvae towards the end of the year, this species was absent from samples in 1970. Evidence of a small overwintering population was found from the beginning of 1971 with all larvae developing to the fourth instar by early March and emerging as adults by mid-April. Larvae reappeared in samples during mid-May with evidence of a period of emergence during June. Subsequent cohorts are more difficult to define but there are indications of 3 periods of recruitment of young larvae, in July, August and September. No fourth instar larvae were found after the beginning of November, but a small population of second instar larvae persisted to the end of the year. *O. fulva* thus appeared to have 5 generations: an overwintering generation which persisted from October to April, a well-defined spring generation and 3 overlapping summer/autumn generations.

Subfamily CHIRONOMINAE

Paratendipes albimanus (Meigen)   Fig. 7

This was the only species to have a single generation, the timing of which was identical in the 2 years, although the number of larvae was much smaller in 1971.
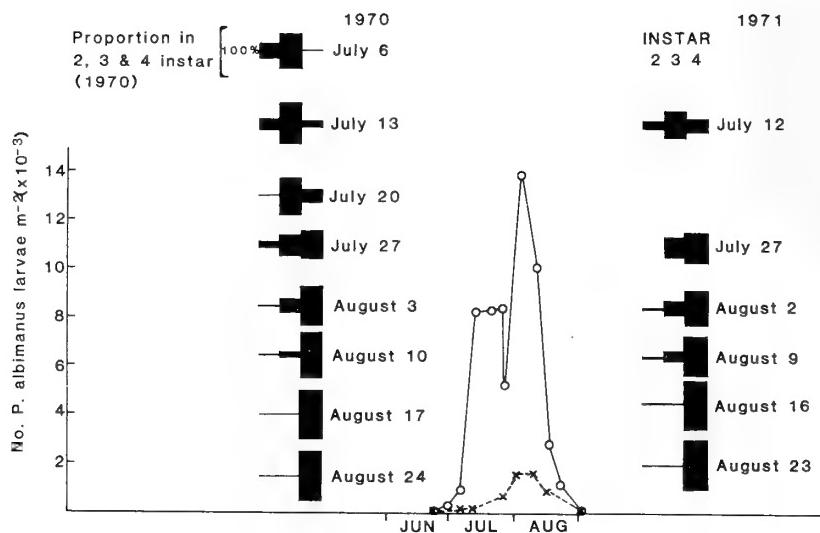
FIG. 7.   Population density of *P. albimanus,* with proportion in instars 2-4 on successive sampling dates. Solid line = 1970 data, broken line = 1971.

Larvae first appeared in significant numbers in July, reached a peak early in August and had virtually disappeared by the end of August. Otherwise only very occasional first and second instar larvae occurred in samples.

This life-cycle is very similar to that described for the same species living in a Michigan headwater-stream by Ward and Cummins (1978) and also corresponds with Lehmann's (1971) description of a flight period during July and August on the Fulda.

Ward and Cummins (1978) found that in their situation the population overwintered as first and second instar larvae. The few larvae which were found in the Tadnoll Brook in months other than June, July and August were all early instar which suggests that a similar situation exists here.

Paracladopelma camptolabis Kieffer   Fig. 8

No trace of an overwintered population was found in early 1970. A clearly defined generation was evident from late May, emerging in July and 2 periods of recruitment of young larvae were apparent in late summer and a further period of recruitment in October gave rise to the overwintering population. This pattern was repeated almost precisely in 1971 except that the overwintering population persisted and was considerably augmented in late February/March, presumably by immigration from upstream.

Thus, the life-cycle consists of an overwintering generation, emerging in April, a well defined early summer generation and 2 strongly overlapping generations in late summer, early autumn.
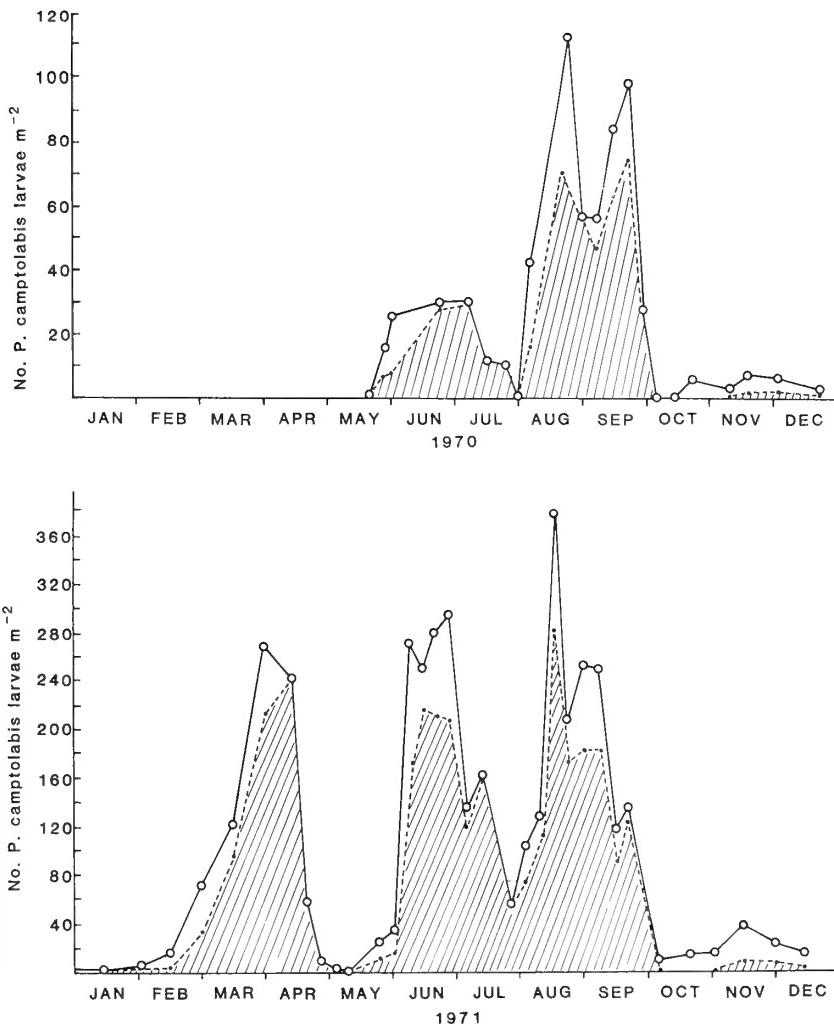
FIG. 8. Population density of *P. camptolabis*. Solid line = all larvae, broken line = fourth instar only.

Polypedilum convictum (Walker)   Fig. 9

Trends in population density of this species were very different between the 2 years. In 1970, larvae first appeared in mid-June with 2 overlapping but reasonably well-defined generations between then and mid-September; whereafter no further larvae were found until March of the following year.

Second and third instar larvae were found during March 1971 with fourth instars appearing early in April. By the end of April all larvae were in the
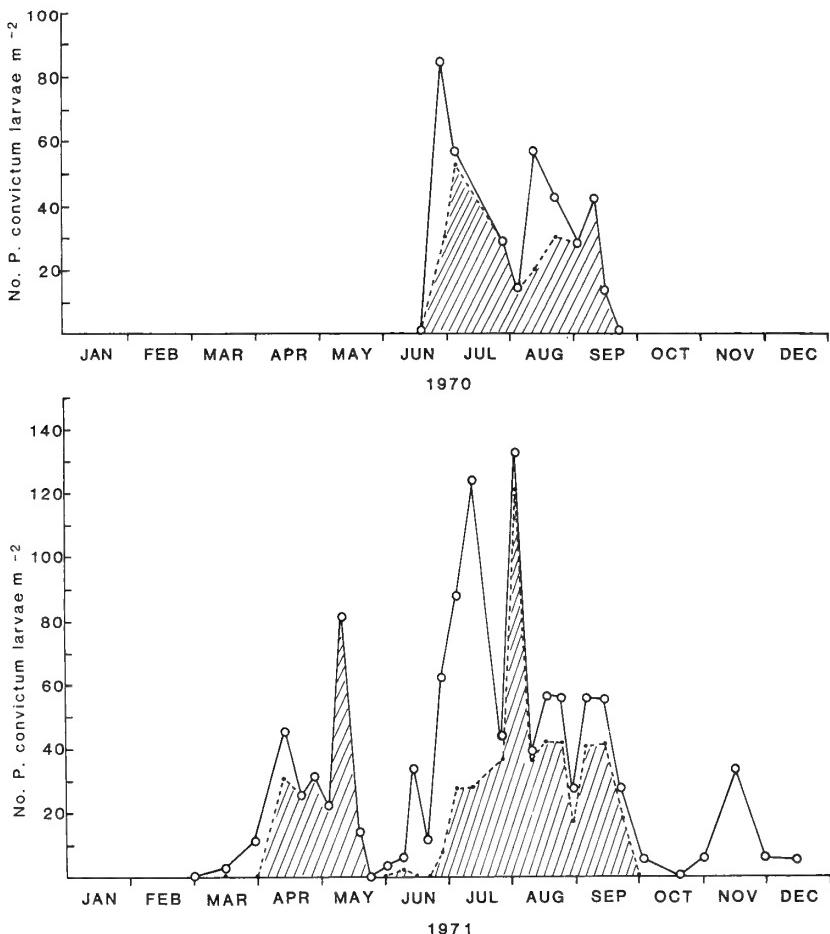
FIG. 9.   Population density of *P. convictum*. Solid line = all larvae, broken line = fourth instar only.

fourth instar and emergence was completed by late May. Two periods of recruitment of young larvae were apparent during the summer, the first in June/July giving rise to an emergence in August, and the other in August and September, corresponding respectively with the 2 generations observed in 1970.

An autumn population first appeared in October and persisted as second instar larvae until the end of the year. Evidently this represented the over-wintering generation.
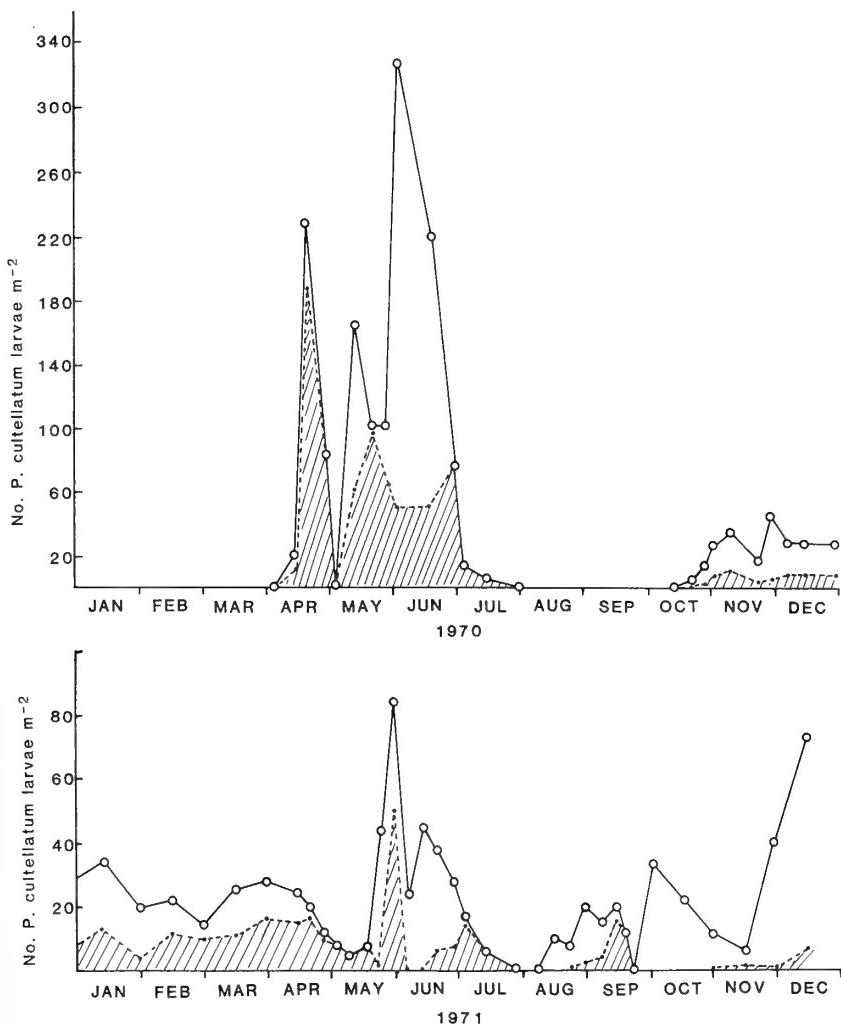
FIG. 10.   Population density of *P. cultellatum*. Solid line = all larvae, broken line = fourth instar only.

On occasions large fluctuations in the density of larvae occurred which were not obviously related to emergence or to recruitment through oviposition. In late July there appears to have been a mass emigration of third instar larvae, compensated for by immigration of fourth instar larvae shortly afterwards. A similar explanation probably applies to the temporary drop in numbers in late August, though on this occasion the differences were not

statistically significant. Presumably such movements are initiated by local changes in environment. It is not possible to say what these changes were but discharge can be eliminated as a possibility since it was more or less constant over the period in question.

Polypedilum cultellatum Goetghebuer   Fig. 10
    A well defined peak in numbers of this species occurred in late April 1970, most of which were fourth instars and had disappeared by early May. These larvae must have entered the study reach in the drift and probably represented the tail-end of an overwintered generation. Subsequently, there was evidence of 2 overlapping generations between May and July. No larvae were found during August or September 1970, but a population of third and fourth instar larvae appeared in October and persisted over winter, emerging in late April or early May. Subsequent trends were similar to those of the previous year, except that larvae of an additional, distinct generation were present during August and September.

Cladotanytarsus vanderwulpi Edwards   Fig. 11
    Small numbers of this species occurred in April in both years and gave rise to an emergence in late April/early May. Subsequent clearly defined, separate generations occurred in June/July and August/September. Whereas there was no sign of a generation overwintering from 1970, a large number of second instar larvae persisted to the end of 1971. It is probable that the relatively small number of larvae, all fourth instar, which were found in March and April of 1970 and 1971 represented immigrants from a population which overwintered upstream of the sampling reach. The species thus has a protracted overwintering generation extending from October to April followed by 2 well defined summer generations.

DISCUSSION

    A range of life-cycles is discernible amongst the species considered, from the single annual generation of *P. albimanus* through to the probable 5 of *Odontomesa fulva*. In only 3 species, *P. albimanus, P. olivacea* and *C. vanderwulpi* with 1, 2 and 3 generations respectively, were all generations distinct. In all other species they overlapped more or less strongly for at least part of the year. Usually this was during late summer and early autumn, but in the case of *P. cultellatum* it was the 2 early summer generations which overlapped, the later one being distinct. Both this species and *P. convictum* occur in relatively large numbers in the Tadnoll Brook and they apparently occupy similar niches. In this context, it is interesting to note that the life-cycle of *P. cultellatum* enabled it to have 2 generations in early summer in advance of the summer generation of *P. convictum*.
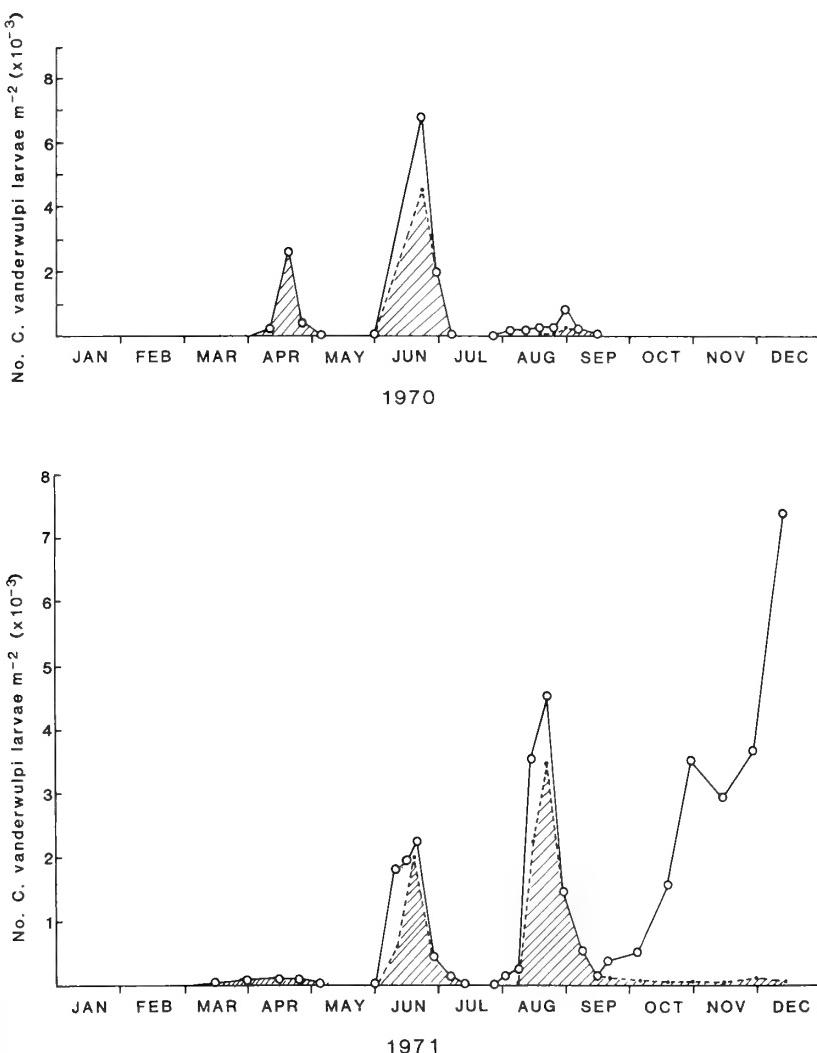
FIG. 11. Population density of *C. vanderwulpi*. Solid line = all larvae, broken line = fourth instar only.

Development times for each generation may be estimated with reasonable accuracy for most species using the available data. The overwintering generation generally occupied about 30 weeks (28 to 33), the only outstanding exception being *O. fulva* which required only about 24 weeks to complete this part of its life-cycle. For those species with more than 2 annual

generations, development time varied between 6 and 13 weeks in spring and early summer and 5 to 10 weeks later in the summer and early autumn.

In many cases, recruitment of larvae was evident in late winter or early spring indicating that immigration had occurred from upstream. Similarly in 1970, the autumn generation of *P. cultellatum* was lacking at the study-site, but an overwintering generation was present from mid-October onwards. In this instance, the overwintering population must either have been derived from larvae entering the reach in the drift or from oviposition by immigrant females.

The general point arising from this variability is that a particular site may not be consistently suitable for colonization by a particular species so that observations made at one site, especially over a restricted period of time, are liable to produce an incomplete picture and lead to erroneous conclusions regarding life-cycles. Ladle *et al.* (1977) also noted variation in the number of generations of *Simulium* spp. apparent at different sampling sites.

In this present study, several species of chironomid showed no indication of a population overwintering from 1969 or 1970. In contrast, all species maintained relatively high population densities to the end of 1971. An unusual feature of the latter months of 1971 was the lack of any significant increase in discharge. The study reach was an almost straight channel with rather uniform cross-section of steep banks and flat bottom. A spate is therefore likely to influence the entire reach in a uniform manner. Other sections of stream, incorporating meanders and deeper pools would be more variably affected and be more likely to retain suitable habitats.

The 2 tanypodine species are particularly prone to be washed out by spates since their preferred substratum of organic detritus can only persist in regions of low water velocity. In 1970 the number of *P. choreus* however, declined well before the onset of autumn floods. *P. choreus* larvae were shown to overwinter mainly as second instars whereas *A. trifascipennis* overwintered in the third and fourth instar. The smaller size of overwintering *P. choreus* larvae made them suitable prey for *A. trifascipennis* and their remains were frequently found in the guts of the latter species.

The apparently consistent life-cycle of *Paratendipes albimanus* in rivers in Canada and Europe is particularly interesting in view of the work of Ward and Cummins (1979) which showed that the life-cycle can be modified by altering the quality of food given to the larvae and their observation that in lakes this same species apparently has 2 annual generations.

References

FITTKAU, E.J., F. REISS AND O. HOFFRICHTER.   1976.   A bibliography of the Chironomidae. K. norske Vidensk. Selsk. Mus. Gunneria 26:1-177.

FORD, J.B.   1957.   A study of the biology and distribution of mud-dwelling chironomid larvae in a chalk stream. Ph.D. Thesis. (University of Southampton.) 225 pp.

HOFFRICHTER, O. AND F. REISS.   1981.   Supplement 1 to "A bibliography of the Chironomidae." K. norske Vidensk. Selsk. Mus. Gunneria 37:1-68.

LADLE, M., J.A.B. BASS, F.R. PHILPOTT AND A. JEFFERY.   1977.   Observations on the ecology of Simuliidae from the River Frome, Dorset. Ecological Entomology 2, 197-204.

LADLE, M. AND H. CASEY.   1979.   The ecology of southern English chalk streams. Salm. Trout Mag. 217:52-57.

LINDEGAARD-PETERSON, C.   1972.   An ecological investigation of the Chironomidae (Diptera) from a Danish lowland stream (Linding Å). Arch. Hydrobiol. 69:465-507.

PINDER, L.C.V.   1974.   The Chironomidae of a small chalk stream in southern England. Ent. Tidskr. Suppl. 95:195-202.

————.   1980.   Spatial distribution of Chironomidae in an English chalk stream. *In* D.A. Murray (ed.), *Chironomidae, Ecology, Systematics, Cytology and Physiology.* Pergamon Press, Oxford. 153-161.

RINGE, F.   1974.   Chironomiden-Emergenz 1970 in Brietenbach und Rohrwiesenbach. Schlitzer Produktionsbiologische Studien (10). Arch. Hydrobiol. Suppl. 45:212-304.

WARD, C.M. AND K.W. CUMMINS.   1978.   Life-history and growth pattern of *Paratendipes albimanus* in a Michigan headwater stream. Ann. ent. Soc. Am. 71:272-284.

————.   1979.   Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). Ecology 60:57-64.

Chironomid Longitudinal Distribution and Macroinvertebrate Diversity along the Llobregat River (NE Spain)

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ABSTRACT. — Qualitative samples were taken at 18 riffles along the Llobregat river (NE Spain) during August and September 1979 and April 1980. For each sample, the populations and composition of the macroinvertebrate fauna present were considered. Composition of the chironomid fauna, its distribution along the river, and temporal and spatial changes are discussed. The differences between the species-rich communities of the upper and medium riffles, and the simplified communities of the lower river reaches, are a consequence of human disturbance such as flow regulation and pollution. A high correlation exists between the extent of disturbance and changes in species richness and diversity patterns along the river, when these are based on the macroinvertebrate collections and on the relative abundance of each species in the sampled communities. The patterns are similar to those predicted by the "Intermediate Disturbance Hypothesis" (Ward & Stanford 1983). The importance of completing the classification of Chironomidae to the same taxonomic level as the other macroinvertebrates, before any general speculation can be made regarding species richness and diversity patterns along the rivers, is discussed.

INTRODUCTION

Chironomidae are an important component of the macroinvertebrate fauna in rivers, streams and brooks, and considerable work has been devoted to the identification of species living on stones in riffle areas. Therefore, the community structure is well known for some European and American rivers (Thienemann, 1954; Lindegaard, 1972; Lehmann, 1971; Lesage & Harrison, 1980; Laville, 1981). Some of these studies were based primarily on the collection of pupal exuviae or on the use of adult emergence traps, due to the difficulty of larval species identification, especially those of the *Cricotopus-Orthocladius* group. (Hirvenoja, 1973; Soponis, 1977; Kownacki & Zosidze, 1980).

This is the first study of the chironomids of a Spanish river although some previous information is available regarding riverine species caught near different Catalonian rivers (Prat, 1976) and Spanish reservoirs (Prat, 1979, 1980). In this work we present the species composition and longitudinal distribution of chironomid larvae in the river Llobregat (NE

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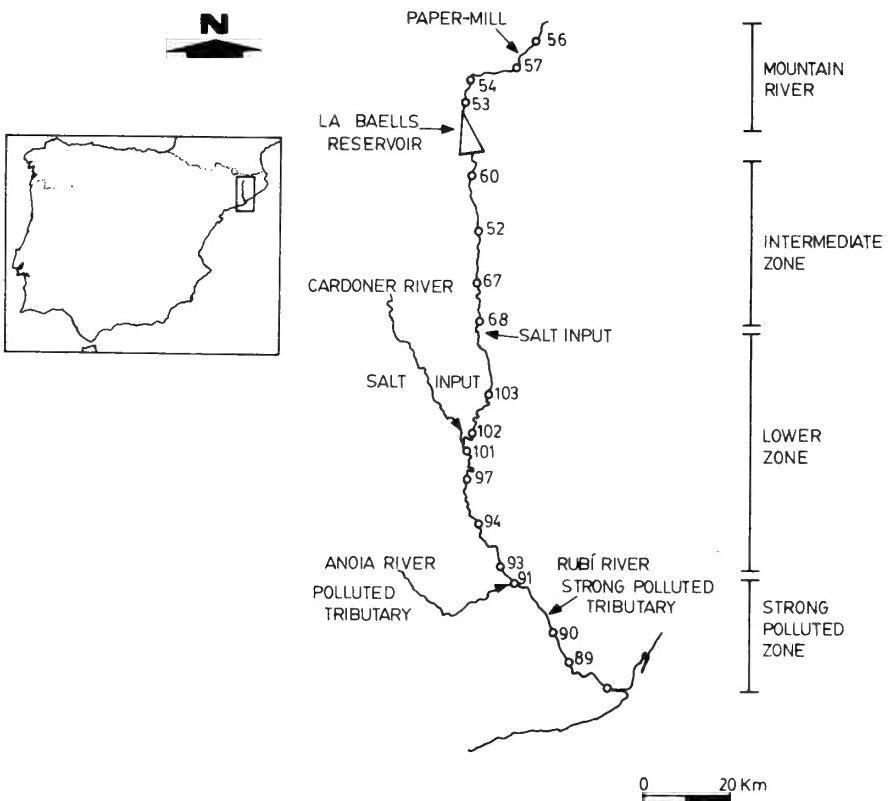
FIG. 1.   Location of the river Llobregat and sampling points along the river. The most striking features affecting macroinvertebrates are indicated.

Spain). We shall also discuss the importance of having a correct generic or specific identifications of the larvae, if one wishes to recognize the diversity patterns of the invertebrate fauna along the rivers.

STUDY AREA

The river Llobregat is located in Catalonia (NE Spain). It is a typical mediterranean river 145 km. long, with a mean annual discharge of 700 Hm³ and characteristic seasonal changes in flow with maxima in spring and fall and reduced flow in summer (Prat *et al.,* 1982). The river flow is regulated from up stream by the "La Baells" dam with a storage capacity of 125 Hm³. Many weirs, built in the XIX century to provide electrical power

to textile mills, are present along the river course. Water is alkaline, and domestic and industrial effluents enter the river especially in its lower stretches. Detailed information concerning the morphological, physical and chemical characteristics of the river is included in Puig *et al.* (1981), and Prat *et al.* [1982, and 1983 (in press)].

METHODS

Eighteen sampling stations were established along the river (Fig. 1). At each station 23 physico-chemical measurements were taken, together with macroinvertebrate samples. Each station was visited in September and December of 1979 and in April of 1980.

An extensive effort was undertaken in order to collect most of the species present on stones. Only rocky fast-current zones were studied, using stratified samples (Resh, 1980). Material was preserved and later sorted in the laboratory. In the sorting process, we routinely counted the animals present and made the assumption that the relative proportions of the different species in the sample reflected their relative abundance on stones. The data were used to attempt a quantification of diversity. In any case, a minimum of 200 individuals were sorted, counted and identified, and at least 100 chironomid larvae were identified from each sample.

RESULTS

Chironomid components of the fauna and longitudinal distribution. — Larvae of the Chironomidae were diverse and abundant in all 18 stations along the river. Pupae, occasionally found and some of these, were males with fully developed genitalia; therefore, the most common larval types could be identified to species. The associations were found after the examination of all pupae present in the samples. In many cases, the larval exuvia was attached to a male pupa permitting clear larval-pupal-adult association. In other cases, however, it has been impossible to identify the larvae to the specific level, especially in some scarce larvae of the *Eukiefferiella* and *Cricotopus-Orthocladius* group (Fig. 2).

The pattern of species distribution in three different seasons emphasizes the importance of seasonal change (Fig. 2). Some species are rare in summer or winter (as *Eukiefferiella sp.* I, *Eukiefferiella claripennis* or *Nanocladius rectinervis*) and common in spring (April 1980).

Other species seem to be found only in certain parts of the river. *Diamesa* spp. with *Paracricotopus niger* and *Parorthocladius nudipennis* are common only upstream from the La Baells reservoir (sampling point 60). On the
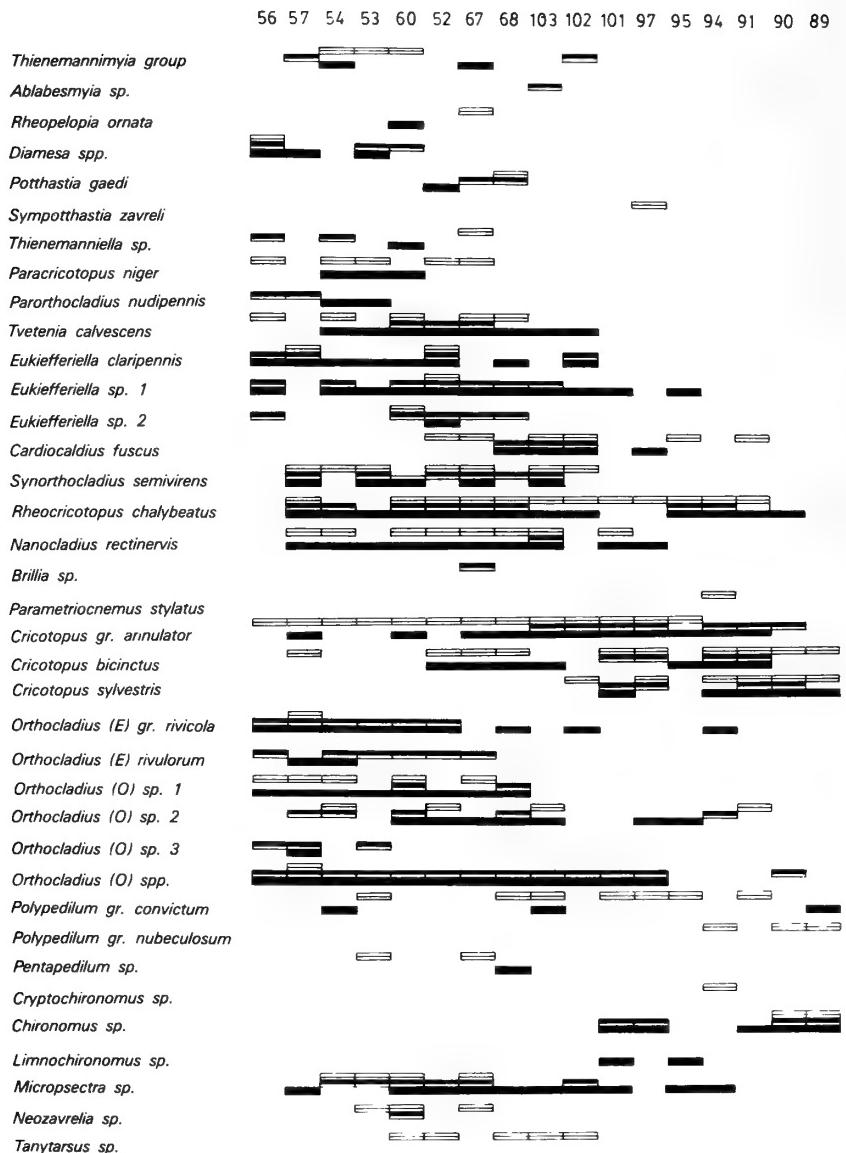
FIG. 2. Longitudinal distribution of chironomids along the Llobregat at three different seasons of the year. September 1979; upper-white lined rectangles. December 1979; Middle-upper half black-rectangles. April 1980; Lower all black rectangles.

other hand, *Synorthocladius semivirens, Nanocladius rectinervis,* and *Tvetenia calvescens* are more frequent in the intermediate reaches, between the sampling points 60 and 67 (Fig. 2). *Isocladius sylvestris, Chironomus* sp. and *Cricotopus bicinctus* are common in the lower parts of the river. Data about the relative abundance of the different species will be presented in Prat *et al.* (1983, in press).

Species richness and diversity. — Species richness and diversity indices have been used in many invertebrate surveys on rivers (Bournaud & Keck, 1980) as a measure of the community structure. One of the most widely used indexes is the Shannon's (Statzner, 1981) which some authors (Cook, 1976; Godfrey, 1978) state to be inversely correlated with the water pollution. One of the problems encountered in the use of such an index to macroinvertebrate collections is the taxonomic level of identification. Normally, in papers concerning species richness or diversity of the macroinvertebrates in rivers, the identification level is not the same for all the organisms sampled, especially in the Chironomidae, which, despite their abundance, are considered, in most cases, only to the family level. For these reasons, absolute values in number of species or diversity can be very different as we found in the Llobregat.

In this river, the richness of the invertebrate fauna (sensu Ward & Stanford, 1981) at three distinct times of the year (Figs. 3 and 4), presents a quite different set of values depending on whether we consider all the Chironomidae as a single taxon (Fig. 3) or whether each midge species is individually identified (Fig. 4). However, the pattern of the total species number along the river may be very similar in both cases, with the maximum richness in the upper and middle reaches (Figs. 3 and 4, stations 54 to 67). If the chironomids are identified as separate species, richness in station 60 (Fig. 4) is very close to the value found by Ward (1974) below deep-release reservoirs. This station is 4 km. downstream La Baells reservoir and the water temperature is influenced by the hypolimmical water released from the dam (Prat *et al.,* 1982, Fig. 16 Puig *et al.,* 1981).

The relative number of Chironomidae is also very important in all the stations along the river. The diversity indices of all the macroinvertebrate groups including the Chironomidae, as a single taxon (Fig. 5), are obviously lower than the indices computed with due consideration to the relative proportion of the different midges listed in Fig. 2 (Fig. 6). All the species names of the macroinvertebrates and their relative abundance in the samples on September 1979, can be found in Prat *et al.,* (1983, in press).

With regard to the diversity pattern along the river, no differences appear to exist in it whether the Chironomidae are included as a unique taxon or counted by species. In both cases, this pattern parallels the total species richness (Figs. 3 to 6). On the other hand, the absolute values of the diver-
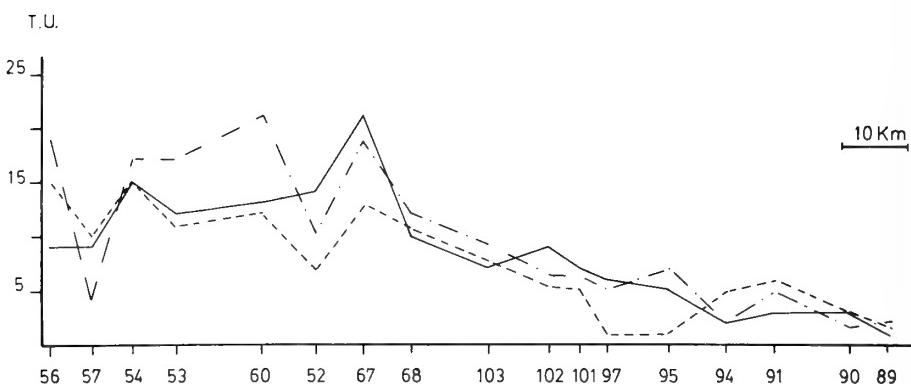
FIG.3.   Number of taxonomic units of macroinvertebrates along the Llobregat if the Chironomidae are included as a single taxon. Solid black line—September 1979; dashes—December 1979; dot and dash line—April 1980.
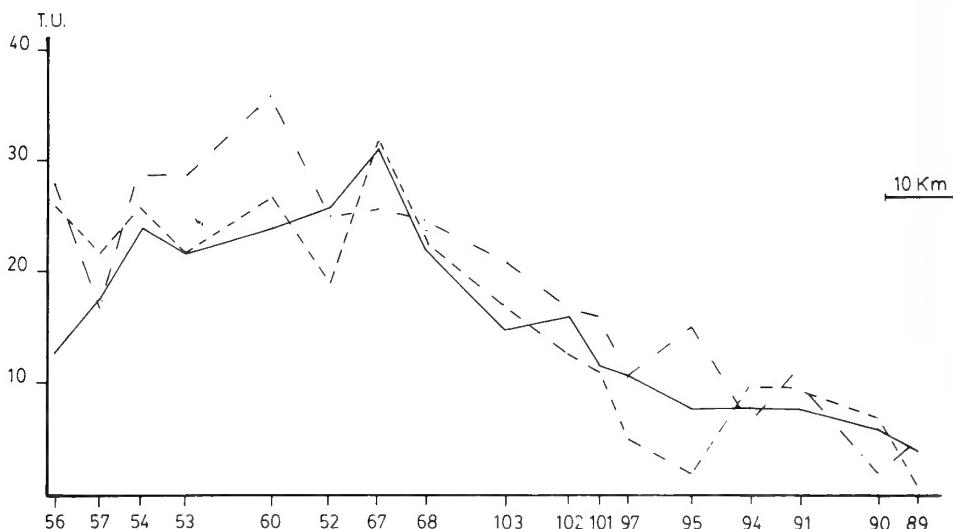

FIG. 4.   Number of taxonomic units along the Llobregat. Chironomids are entered as the numbers of species listed in Fig. 2. Linear symbols as in Fig. 3.

sity vary in each case. If we consider the Chironomidae as a single taxon, the highest diversity score is 3 bits and only a few sampling points have diversities over 2 bits (Fig. 5). If we take into account the relative presence of the different chironomid species, the highest diversity is close to 4 bits and diversities under 2 bits are only frequent in the lowest and very polluted part of the river (Fig. 6).

Thus, a general increase in the diversity index is produced if we determine Chironomidae to the same taxonomic level as the other groups. In this sense, if we are to attempt to give an accurate picture of real species richness and its diversity pattern along the rivers, it is necessary to identify the chironomids to species.

DISCUSSION

The river zonation versus the river continuum concept. — Although many attempts have been made to provide a detailed picture of the rivers (hydrologic, morphometric and even the water quality) only broad, imprecise zones have been established. One of these attempts is the zonation of the rivers using the macroinvertebrates (the Illies & Botosaneanu system). This is based on the presence-absence data of some species in the different sampling points. As a result "rithron" and "potamon" zones can be defined.

In the Llobregat, despite the seasonal fluctuations, the longitudinal distribution of the macroinvertebrates, including chironomids, allows us to divide the river into different zones (Prat *et al.,* in press, and Fig. 1). The higher, intermediate and lower zones can be easily recognized in the river, either by the water quality criteria or by the longitudinal distribution of the species.

The reservoir of La Baells is the limit of the typical mountain zone of the Llobregat (Fig. 1 St. 60). The input of salt after station 68 represents a turning point in the ecology of the river, and after station 91 the strong pollution inputs limit the fauna to just a few resistant species. These zones can be defined by presence of characteristic species in each section but also by the relative abundance of the species.

Diverse authors have pointed out the difficulties in applying Illies & Botaseneanu (1963) methodology to some rivers (Hawkes, 1975). This occurs because of the lack of any discontinuity, so that the river can be defined as a continuum, where the species are replaced successively along its course and no definite zones can be established. The so-called "river continuum concept" (Vannotte *et al.,* 1981; Hawkins & Sedell, 1981) has been applied successfully to some American rivers but as Ward & Stanford (1983) have pointed out, the applicability of the "river continuum concept" to the majority of the streams and rivers is very difficult, because in most cases these are altered by the human activities as dams, weirs or pollution. The changes can be so striking that all the community structure is altered, even in short distances, although different "zones" can be distinguished in the pattern of the species distribution looking to the fluvial ecosystem as a
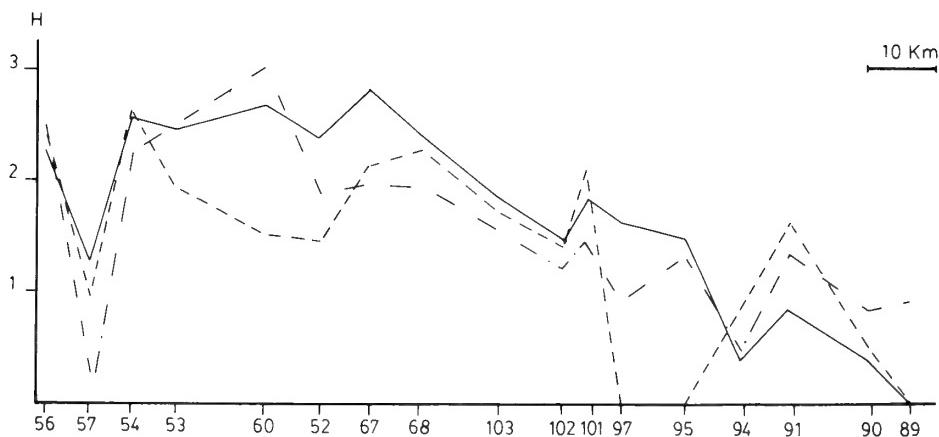
FIG. 5. Shannon diversity of the macroinvertebrate communities along the Llobregat calculated on the basis of the relative presence of the different taxonomic units, considering the chironomids as a single taxonomic group. Linear symbols as in Fig. 3.
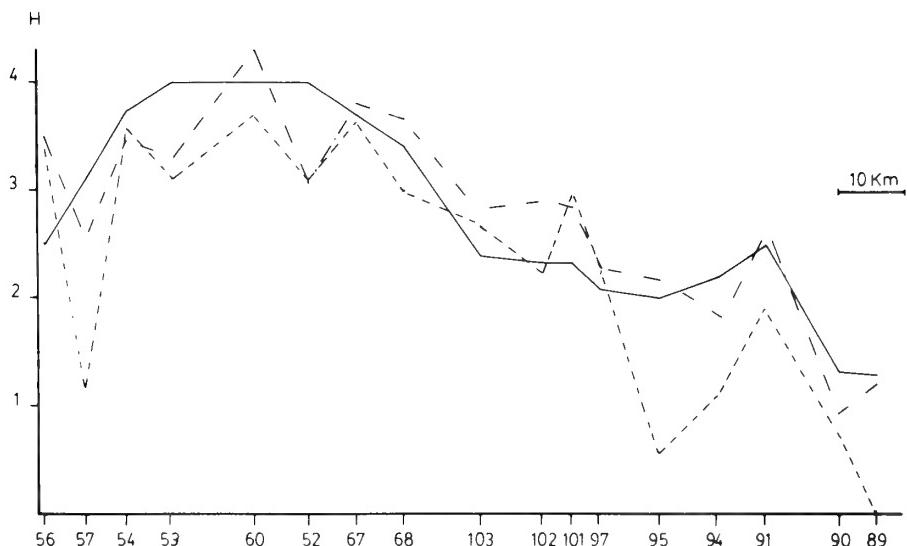

FIG. 6. Shannon diversity of macroinvertebrate communities along the Llobregat, when the chironomids are entered as the taxonomic units of the Fig. 2. Linear symbols as in Fig. 3.

whole. In the case of river Llobregat the "river continuum concept" cannot be applied because of the great human impact. On the other hand, the idea of "Intermediate Disturbance Hypothesis" seems to be part of our pattern of species richness and diversity.

The disturbance in the Llobregat, and the patterns of species richness and diversity along the river. — In the Llobregat the disturbance by man is diverse and frequent (Prat *et al.,* 1982). It changes the patterns of species distribution, species richness and the relative presence of the species. However, criteria still exist that allow us to recognize different zones (Prat *et al.* 1982). These zones were recognized, as we have noted previously, by using the Illies and Botosaneanu (1963) criteria.

As we have seen before, the species richness runs parallel to the pattern of diversity (Figs. 3-6) and both seem to be related to the disturbance level. The already defined zones along the Llobregat, can be delimitated by the external influences, and associated with the sharp changes in species richness and diversity (see for instance the differences between the sampling points 68 and 103 before and after the salt inputs). Therefore, the patterns of the species richness and diversity are well correlated to the level of disturbance in each sampling point or zone. We can then consider the faunal richness fluctuations within the frame of disturbance level.

At its origin (station 56) the Llobregat is undisturbed and the low water temperature is almost constant (Prat *et al.,* 1982, Fig. 16). Species richness is not high, and as the relative abundance of each species is very low, the diversity can reach high values (Figs. 4 and 6).

At station 57, the Llobregat is still a mountain river, but the water quality has been strongly affected by a paper mill and by sewage effluents. As a result, species richness decreases (nearly all the species present are Chironomidae as can be seen by comparing Figs. 3 and 4) along with diversity.

Higher species richness and diversity are regained by the river between stations 53 and 54, where no human influence is present. The dam (station 60) increases the species richness and diversity in the river (Figs. 4 and 6), probably as a result of the regulation of the flow and damping of temperature fluctuations.

A sharp decrease in species richness and diversity takes place between stations 67 and 103 (Figs. 4 and 6). Here the river receives salt from mining activity and organic pollution increases. The disturbance is followed by a decrease of the richness and diversity of some very abundant species, especially *Hydropsyche exocellata* (Trichoptera).

A great change in the quality of water occurs when the Llobregat receives some tributaries in its lower part, and the input from sewage and industrial

effluents in the area around Barcelona (sampling points 89 and 90). Few species occur in these zones, mainly chironomids and tubificids.

Despite the lack of a more accurate quantitative data and the broad periods between samples, species richness and diversity patterns seem to agree with the basic idea of the "Intermediate disturbance hypothesis" given by Ward & Stanford (1983) as applied to rivers. Higher diversity is found in areas with an intermediate disturbance (st. 53 to 67), more than in very constant conditions (station 56) or when the disturbance is very great (stations 57, 103, 94) or even extreme (station 91 to the mouth). The Llobregat seems to answer to human impact-increasing or keeping a higher species richness and diversity when the extent of such actions is moderate (according to the flow conditions), and impairing the community structure when the disturbance is greater.

The application of some ideas like the "Intermediate disturbance hypothesis" can be a helpful instrument for generalization in the very disturbed rivers, as are those of the Mediterranean basin, and could be an alternative to "river zonation" or "river continuum" concepts.

In any case, one should not attach excessive importance to species richness and diversity until an equivalent degree of taxonomic level is reached in the different macroinvertebrate groups considered in macroinvertebrate surveys. In some cases, as in the Llobregat, we cannot dispense with the most frequent and abundant group, the Chironomidae, despite the systematic difficulties involved.

REFERENCES

BOURNAUD, M. AND G. KECK. 1980. Diversite specifique et structure des peuplements de macro-invertebres benthiques au long d'un cours d'eau: le Furans (Ain). Acta Oecologica Oecol. Generalis. 1:2:131-150.

COOK, S.E. 1976. Quest for an index of community structure sensitive to water pollution. Environ. Pollut. 11:269-288.

GODFREY, P.J. 1978. Diversity as a measure of benthic macroinvertebrate community response to water pollution. Hydrobiologia 57:2:111-122.

HAWKES, H.A. 1975. River zonation and classification. In: B.A. Whitton (ed.), River ecology, Blackwell Scientific Publications, Oxford. 725 pp., pp. 313-374.

HAWKINS, C.P. AND J.R. SEDELL. 1981. Longitudinal and seasonal changes in functional

.organization of macroinvertebrate communities in four Oregon streams. Ecology 62:387-397.

HIRVENOJA, M. 1973. Revision der gattung *Circotopus* van der Wulp und ihrer Verwandten (Diptera, Chironomidae). Ann. zool. fenn. 10:1-363.

ILLIES, J. AND L. BOTOSANEANU. 1963. Problemes et methodes de la classification et de la zonation ecologique des eaux courantes, considerees surtout du pont de vue faunistique. Mitt int. verein. Limnol. 12:57 pp.

KOWNACKI, A. AND R.S. ZOSIDZE. 1980. Taxocens of Chironomidae (Diptera) in some rivers and streams of the Adzhar ASSR (Litte Caucasus Mnts). Acta Hydrobiol. 22:1:67-87.

LAVILLE, H. 1981. Récolte d'exuvies nymphales de chironomides (Diptera) dans le haut-Lot de la source (1295 m), au confluent de la Truyère (223 m). Annls. Limnol. 17(3):225-289.

LEHMANN, J. 1971. Die Chironomiden der Fulda. Systematische, Okologische und faunistische Untersuchungen. Arch. Hydrobiol. Suppl. 37:466-555.

LESAGE, L. AND A.D. HARRISON. 1980. The biology of *Cricotopus* in an algal enriched stream: Part. 1. Normal biology. Arch. Hydrobiol. Suppl. 57:375-418.

LINDEGAARD-PETERSEN, C. 1972. An ecological investigation of the Chironomidae (Diptera) from a Danish lowland stream (Linding A). Arch. Hydrobiol. 69:465-507.

MARGALEF, R. 1981. La Biosfera, entre la termodinámica y el juego. Omega. Barcelona. 236 pp.

PRAT, N. 1977. Quironómidos de Catalunya Graellsia XXXI: 157-185.

──────────. 1979. Quironómidos de los embalses españoles (1) Graellsia XXXIII:37-96.

──────────. 1980. Quironómidos de los embalses españoles (II) Graellsia XXXIV:59-119.

PRAT, N., M.A. PUIG, G. GONZALEZ AND M.J. TORT. 1982. Predicció i control de la qualitat de les aigües dels rius Besós i Llobregat. I: Els factors fisics i quimics del medi Monografies 6:206 pp. Servei del medi ambient de la Diputació de Barcelona.

PRAT, N., M.A. PUIG, G. GONZALEZ, J.M. TORT AND M. ESTRADA. in press. The Llogrebat: A mediterranean river fed by the Pyrenées. *In:* B.A. Whitton (ed.), The ecology of European rivers. Studies in Ecology. Blakwell. London.

PUIG, M.A., I. BAUTISTA, M.J. TORT AND N. PRAT. 1981. Les larves de trichoptères de la rivière Llobregat (Catalogne, Espagne). Distribution longitudinale et relation avec la qualité de l'eau. Proc. of the 3rd Int. Symp. on Trichoptera. G.P. Moretti (ed.). Series entomologica, Vol. 20, Dr. W. Junk Publishers, 303-309 pp.

RESH, V.H. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect estudies. J. Fish. Res. Board. Can. 36:290-341.

SOPONIS, A. 1977. A revision of the nearctic species of *Orthocladius* (*Orthocladius*) van der Wulp (Diptera: Chironomidae) Mem. Entomol. Soc. Canada. 102:187 pp.

STATZNER, B. 1981. Shannon-Weawer diversity of the macrobenthos in the Schierenseebrooks (North Germany) and problems of its use for the interpretation of the community structure. Verh. Internat. Verein. Limnol. 21:782-786.

THIENEMANN, A. 1954. *Chironomus*. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewässer 20:834 pp.

VANNOTE, R.L., G.W. MINSHALL, K.W. CUMMINS, J.R. SEDELL AND C.E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

WARD, J.V. 1974. A temperature stressed stream ecosystem below a hypolimnial release mountain reservoir. Arch. Hydrobiol. 74:247-75.

WARD, J.V. AND R.G. DUFFORD. 1979. Longitudinal and seasonal distribution of macro-

invertebrates and epilitic algae in a Colorado springbrook-pond system. Arch. Hydrobiol. 86:3:284-321.

WARD, J.V AND J.A. STANFORD.   1983.   The intermediate disturbance hypothesis: An explanation for biotic diversity patterns in lotic ecosystems. *In:* T.D. Fontaine and S.M. Bartell (eds.), Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Mich. 347-356.

Three New Species of Lopescladius Oliveira, 1967

(syn. "Cordites" Brundin, 1966, n. syn.),

with a Phylogeny of the Parakiefferiella group

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ABSTRACT. — LOPESCLADIUS Oliveira, 1967 is shown to be the valid name for *Cordites* Brundin, 1966, illustrated from pupa. Diagnoses for all stages are given. Males and pupae of two new species, *Lopescladius fittkaui, Lopescladius verruculosus,* the male of one new species *Lopescladius inermis,* and the pupae of six more species are described. The mainly Neotropical (, but also Nearctic) *Lopescladius* is shown to be a member of the *Parakiefferiella* group *(Lopescladius, Gynnidocladius* Subl. et Wirth, *Rheosmittia* Brund., *Parakiefferiella* Thien., *Stilocladius* Rossaro, *Saetheriella* Halv., *Krenosmittia* Thien., *Epoicocladius* Zavř.) with *Gynnidocladius* from the subantarctic Campbell Island as its sister genus. *Rheosmittia* apparently form the sister group of these two genera combined.

Male imagines of *Lopescladius* Oliveira associated with numerous pupal exuviae and collected by D. E.J. Fittkau, Zoologisches Staatssammlung, Munich, from Brazil and Mexico were sent me by Dr. F. Reiss, also of Zoologisches Staatssammlung, for description of the pupal stage. A closer examination revealed that the pupae were identical to *"Cordites"* Brundin as described by Brundin (1966) on pupae only and thus an invalid name. The specimens from near Manaus in Brazil, and from near Tocuman in Mexico, belonged to two closely related species both apparently differing from the only previously described species, *Lopescladius minutissimus* Oliveira. Later I received pupal exuvia collected by Dr. Fittkau from Peru and Brazil and belonging to yet another six species. Dr. W.P. Coffman, University of Pittsburgh, in collaboration with Dr. S.S. Roback, The Academy of National Sciences, Pittsburgh, is describing all stages of a new species of *"Cordites."* I received mature pupae from Dr. Coffman for comparison. Although the male genitalia of their species is quite dissimilar, the remaining male characters as well as the pupae clearly show that also this species is congeneric with *Lopescladius,* but possibly deserve a separate subgenus. After presenting this paper I received the male of an additional new species from Dr. Ferrington, University of Kansas.

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The general terminology in the following descriptions follows Sæther (1980). The measurements are given as ranges followed by a mean when three or more specimens are measured; n = number measured. The types are deposited in the Zoologisches Staatssammlung, Munich (ZSM) and Museum of Zoology, Bergen (ZMBN).

Lopescladius Oliveira, 1967:417

Cordites Brundin, 1966; 428, invalid name I.C.Z.N. 13b, n. syn.
Unknown gen. & sp. near *Corynoneura;* Roback 1953:113.

Type species: Lopescladius minutissimus Oliveira, 1967:417, by original
    designation.

Other included species: Lopescladius fittkaui n. sp., *Lopescladius inermis* n. sp., *Lopescladius verruculosus* n. sp., *Lopescladius* sp. *A* (pupa), *Lopescladius* sp. *B* (pupa), *Lopescladius* sp. *C* (pupa), *Lopescladius* sp. *D* (pupa), *Lopescladius* sp. *E* (pupa), *Lopescladius* sp. *F* (pupa), *Lopescladius* n. subgen., n. sp. (Coffman and Roback in prep.).

Diagnostic characters. — The combination of strongly protruding, but small, strongly pubescent to short haired eyes; reduced antepronotum; wing broad, without costal extension, with R_{2+3} fused with R_{4+5}, high VR, Cu_1 straight, and squama bare; cordiform ta_4 and small pulvilli; gonostylus bent medially with apical megaseta absent; inferior volsella minute and spine-like *(Lopescladius s. str.)* or broadly digitiform *(Lopescladius* n. subgen.); and gonocoxite (in *Lopescladius s. str.)* with caudal elongation; easily separates the males from all other orthoclads.

The pupae are characterized by the lack of frontal setae and thoracic horn; the unique leg sheath arrangement with all leg sheaths directed straight backwards with apices joined along sutures; the presence of caudal spines on tergites (I) II-VIII and sternites II-VII ($\female$) or II-VIII ($\male$); the absence of hooklets on tergite II and of pedes spurii A and B; and the anal lobe without fringe, with long, apical, dorsally curved, digitiform, moveable projections each carrying 3 equally long macrosetae.

The larvae are characterized by a long antenna longer than head capsule with a long whip-like ultimate segment; S I bifid; premandible with 1 apical tooth and fine brush; mandible with short apical tooth and 6 inner teeth, setae interna present; mentum with broad median tooth and 5 pairs of lateral teeth; separate, claw-bearing parapods; and procercus with 1 strong anal seta.

Male. — Eyes small, strongly protruding, with microtrichia as long as the height of an ommatid (hence between pubescent and hairy). Antenna with 11-13 flagellomeres; antennal groove reaching flagellomere 4-5; flagellomeres 2, 3, 4 and ultimate with sensilla chaetica; setal plume weak, with one stronger developed and one weakly developed whorl of setae on each flagellomere; AR between 0.4 and 1.3. Temporals apparently absent. Palp 5-segmented,

segments progressively longer, third segment with 1 weak sensillum clavatum. Antepronotum more or less reduced, lobes narrowed medially, separated or in narrow contact, without or with 1 lateral seta. Dorsocentrals few, anterior ones stronger than posterior ones; acrostichals apparently absent; about 2 prealars. Scutellars few, in transverse row. Wing broad, membrane with fine punctation of microtrichia barely visible at 350 X. Anal lobe indicated. Costa not or barely extended, ending between M_{3+4} and Cu_1; R_{2+3} fused with R_{4+5}, partially indicated as a line; vannal fold ends distad, An basad to FCu; Cu_1 straight; brachiolum with 1 setae, other veins and squama all bare. Sensilla campaniformia about 6 at base of brachiolum, 3 below seta, and about 6 at apex of brachiolum; 1 at base of subcosta, 1 on FR, and 1 at base of R_1. Pulvilli very small, but distinct. Comb and hind tibial spurs normal. Pseudospurs and sensilla chaetica absent. BV and SV high, ta_4 strongly cordiform. Setae of abdomen very few, often only 1 very long seta on each tergite. Anal point absent, tergum IX at most with a few weak setae. Phallapodeme well developed, with triangular or rounded aedeagal lobe. Transverse sternapodeme broadly curved to nearly straight with or without weak oral projections. (The preparations of two of the described males are not very good with the apodemes indistinct.) Gonocoxite without inferior volsella or, with a spine-like inferior volsella *(Lopescladius s. str.)*, or with a broadly digitiform, bare inferior volsella *(Lopescladius* undescribed subgenus); with a long *Protanypus*-like apical extension *(Lopescladius s. str.)* or without such an extension *(Lopescladius* n. subgen.) Gonostylus with a more or less distinct median bend, without crista dorsalis and apical megaseta.

Pupa — Minute pupae (1.3-3.3 mm long). Frontal setae absent. Frontal apotome without anterior triangular projection, evenly and weakly rounded to reniform shape, smooth to strongly rugulose. Antennal sheath above pedical without pearls to covered with rugulosity. Ocular field with 1 weak postorbital only. Thoracic horn absent. Dorsocentrals 4, 2 anterior and 2 posterior grouped. Thorax rugulose. Wing sheath smooth or rugulose and reticulate. Leg sheaths all directed straight backwards with apices joined along sutures, front leg sheath ending at conjunctives I/II, mid leg in the middle of tergite II and slightly basad of apex of wing sheath, hind leg ending at conjunctive II/III. Abdomen arched. Tergite I and sternites I and IX without shagreen; tergites II-IX and sternites II-VIII with transverse rows of fine group shagreen to very strong spinules in anterior third to half, with reticulation of polygones often with smaller pattern of more faint polygone reticulation inside. Tergites I (II)-VIII and sternites II-VII ($\female$) or II-VIII ($\male$) with caudal rows of erect spines. Tergite II without hooklets. Conjunctives of tergites and sternites with small distinct to indistinct greyish polygones. Pedes spurii A and B absent. Segment I with 5 pairs of D setae, 3 pairs of V setae and 3 pairs of L setae. Segments II-VII each with 4 hair-like L setae, 1-2 of them very small; segment VIII with 2 hair-like L setae. Setae D_2, D_5, V_3 and V_5 broad, lamelliform; tergite VIII with 3 pairs of D setae. O setae and apophyses absent. Anal lobe without fringe, with long, apical dorsally curved, digitiform, moveable, smooth, wrinkled or rugulose projections each carrying 3 equally long macrosetae. Genital sac also curved dorsad.

Larva — A description will be given by Coffman and Roback (in prep.) and Cranston, Oliver and Sæther (1982).

SYSTEMATICS

The male imago of *Lopescladius s. str.* look strikingly different from other orthoclads. The extremely protruding eyes; the broad wings; the distinctly cordiform, *Cardiocladius*-like ta_4; the absence of a megaseta; and the *Protanypus*-like elongation of the gonocoxite; appears to indicate rela-

tionships with plesiomorphic genera as well as with highly derived genera. Also the pupa is unique, particularly with respect to the leg sheath arrangement and the projections of the anal lobe. The larva is peculiar, but do, however, show some similarities with other genera such as *Rheosmittia* Brundin (Cranston & Sæther in ms).

In the key to male Orthocladiinae by Brundin (1956) *Lopescladius* will key to *Camptocladius* v.d. Wulp from which it, however, differs in a number of significant details. The Cu_1 is straight which contradicts a placement in either of the *Smittia, Parakiefferiella* or *Pseudosmittia*-groups. However, as shown by Sæther (1981) for some species of *Smittia* Holmgr. and *Pseudosmittia* Goetgh., the straight Cu_1 almost certainly is a result of FCu being moved far distad and is not an original plesiomorphous condition. The medially bent gonostylus of *Lopescladius* is very similar to and found only in some members of the *Parakiefferiella*-group namely *Rheosmittia* Brund., *Gynnidocladius* Subl. & Wirth, *Parakiefferiella* Thien., and *Stilocladius* Rossaro (Brundin 1956, Sublette & Wirth 1980, Sæther 1982, Cranston & Sæther in ms). The same genera and *Lopescladius* also have some members with reduced numbers of flagellomeres; all except *Stilocladius* and some *Parakiefferiella,* but with the addition of *Krenosmittia* Thien, have R_{2+3} fused with R_{4+5}; all except *Parakiefferiella,* but with the addition of *Saetheriella* Halvorsen (1982), have pubescent to hairy eyes; and they probably all (the larva of *Gynnidocladius* is not known) have a whip-like ultimate larval antennal segment. The pupal anal lobe have an apical elongation of differing shape in all known pupae of the *Parakiefferiella*-group; the pulvilli are present, but small or vestigial probably in all genera; and the ante-pronotum is somewhat reduced except in *Epoicocladius* Zavř. and in some *Parakiefferiella*. All in all, *Lopescladius* clearly appear to be an aberrant and apomorphic member of the *Parakiefferiella*-group. Whether this group perhaps should include some other genera, particularly of the *Pseudosmittia* group, which share a few of the same apomorphous features cannot be decided without a better knowledge of the immature stages and of the females.

Although the same restrictions applies to the *Parakiefferiella* group as here outlined a tentative shceme of argumentation delineating the cladogensis of the genera can be attempted (Fig. 1). Trends showing the same direction are grouped. The following trends are used (a = apomorphous, p = plesiomorphous):

TRENDS 1 — Eyes reduced, strongly protruding (a); less protruding (p).
— Costal extension reduced (a); long (p).
— Cu_1 secondarily straightened (see above) (a); curved (p).
— Distinctly cordiform ta_4 (a); slightly cordiform to cylindrical ta_4 (see Trends 3) (p).

— Anal point absent (a); present (p).
— Megaseta of gonostylus lost (a); present (p).
— Leg sheath arrangement of pupa unique (see above) (a); normal (p).
— Projections of anal lobe very long and moveable (a); short to long, not moveable (p). (Several other trends could be added)

TREND 2 — Male antenna reduced to 5 nonplumose flagellomeres (a); 11-13 plumose flagellomeres (p).

TRENDS 3 — Slightly to distinctly cordiform ta$_4$ (a); cylindrical ta$_4$ (p).
— Anal point reduced or absent (a); well developed (p).
— Acrostichals and scutal tubercle absent (a); acrostichals and/or scutal tubercle present (The acrostichals may be secondarily reduced also in *Rheosmittia* (see trends 5). Whether acrostichals are present or absent in *Krenosmittia* has not been examined. Other genera of the *Parakiefferiella* group all have acrostichals, or scutal tubercle or tuft.)
— Cu$_1$ straight or at most sharply downcurved at apex (a); Cu$_1$ sinuate (p). (The sinuate Cu$_1$ is a synapomorphy for the *Smittia - Parakiefferiella - Pseudosmittia* groups, and symplesiomorphous within these groups.)

TRENDS 4 — Scutum extending hunch-like forward (a); normal (p).
— Anal macrosetae of pupa absent (a); well developed (p).
    (Although the pupa of *Gynnidocladius* is not known it will in all likelihood not possess the autapomorphies of *Rheosmittia*.)
— D$_5$ of pupal tergites II or III to IV flattened and finely split (a); normal (p).

TRENDS 5 — VR higher than 1.4 (a); VR lower than 1.4 (p). (Secondarily high also in *Epoicocladius*)
— Acrostichals and scutal tubercles absent in all or some species of each genus, i.e. tendency to reduction present (a); present (p).
— R$_{2+3}$ fused with R$_{4+5}$ (a); R$_{2+3}$ not fused (or secondarily fused in some *Parakiefferiella* and in *Krenosmittia*) (p).

TREND 6 — Eyes naked without trace of microtrichia between central ommatids (a); eyes pubescent or hairy (p). (See Trends 11).
    There is some doubt whether *Parakiefferiella* really is monophyletic as male *P. coronata* (Edw.) differ distinctly from the other members. However, the immatures appear quite similar to other members of the genus.

TRENDS 7 — R$_{2+3}$ fused with R$_{4+5}$ in all or at least some species of each genus; i.e. tendency to fusion present (a); R$_{2+3}$ separate and distinct (secondarily fused in *Krenosmittia*) (p).

TRENDS 8 — Anal point narrowed (a); broad-based (p).
— Hind tibial comb very oblique (a); normal (p). (The same tendency to an oblique comb is found also in *Saetheriella*.)
— Anal lobe projection reduced (a); present (p). (This trend is regarded as a secondary reduction since *Stilocladius* possesses the synapomorphies of trend 9.)

TRENDS 9 — Gonostylus with a characteristic median bend (a); normal (p).
— All genera with some members with reduced numbers of flagellomeres (a); 13 flagellomeres (p). (*Epoicocladius gynocera* (Edw.) have completely female antenna. Howver, as the immatures are unknown the placement is uncertain. Furthermore, the complete feminization of the antenna probably cannot be regarded as the same trend as reduction of a few flagellomeres.)

— Ultimate segment of larval antenna long, tapering, thread-like (a); normal (p). (Although the larva of *Gynnidocladius* is not known, this trend probably belongs here.)

TRENDS 10 — Costal extension short (a); long or (in *Lopescladius*) secondarily reduced (p).
— Antenna with straight apical seta (a); without (p). (This trend occurs also in the *Pseudorthocladius* and *Smittia*-groups (Sæther & Sublette 1983, Brundin 1956).)

TREND 11 — Eyes pubescent or hairy (secondarily bare in *Parakiefferiella*) (a); eyes bare (p). (This trend could be interpreted as going in the opposite direction and probably do so in more plesiomorphic groups.)

TRENDS 12 — R_{2+3} fused with R_{4+5} (a); R_{2+3} separate or secondarily fused (see trends 5 and 7).
— Larval antenna 4-segmented (a); antenna 5-6 segmented (p). (Parallelly 4-segmented in *Epoicocladius*, see trend 14.)
— Larval maxillary palp unique, Tanytarsiinae-like (a); normal (p).
— Procercus with 1 elongate anal seta, half the length of the body (a); anal setae equally long (secondarily one long anal seta in *Lopescladius*) (p).
— Pupal thoracic horn beset with scale-like plates ending in spinules (a); thoracic horn when present without plates (p).
(Several other autapomorphics could be added here.)

TREND 13 — Antepronotum reduced, with lobes narrowed medially (a); antepronotum not reduced (p).

TREND 14 — Larval antenna 4-segmented (a); antenna 5-6 segmented (secondarily 4-segmented in *Krenosmittia*) (p).
— Abdomen of larva and pupa with a thick covering of setae (a); normal amount of setae (p). A number of other trends based on the aberrant immatures could be added.

TREND 15 — Anal lobe of pupa with an apical more or less well developed elongation (a); without (p).
A number of trends could be added here. These, however, depend on whether the combined *Heterotrissocladius* and *Cardiocladius* groups forms the sister group of the *Parakiefferiella* group as will be suggested by combining the data in Sæther (1977) and Sæther and Halvorsen (1981) or if another group is a more likely sister group.

A number of trends in the above analysis are partly contradictory. Obviously both parallel selections and underlying synapomorphies (Sæther 1979) obscure the synapomorphies. If the weighting were placed more on characters such as hairy eyes and fusion on R_{2+3} with R_{4+5} instead of on the shape of the gonostylus, the thin ultimate larval segment etc. the placement of the genera from *Krenosmittia* to *Parakiefferiella* could well be different. The placement of *Lopescladius, Gynnidocladius, Rheosmittia* and of *Epoicocladius,* however, seem relatively well founded.

It probably is premature to speculate about the zoogeographical importance of the findings since the actual distribution of many of the genera not is well known. However, the sister group relationship between the mainly neotropical *Lopescladius* and *Gynnidocladius* from New Zealand's subantarctic Campbell Island as well as the fact that *Saetheriella* and *Stilocladius* up to now are known exclusively from the southeastern states and, for the
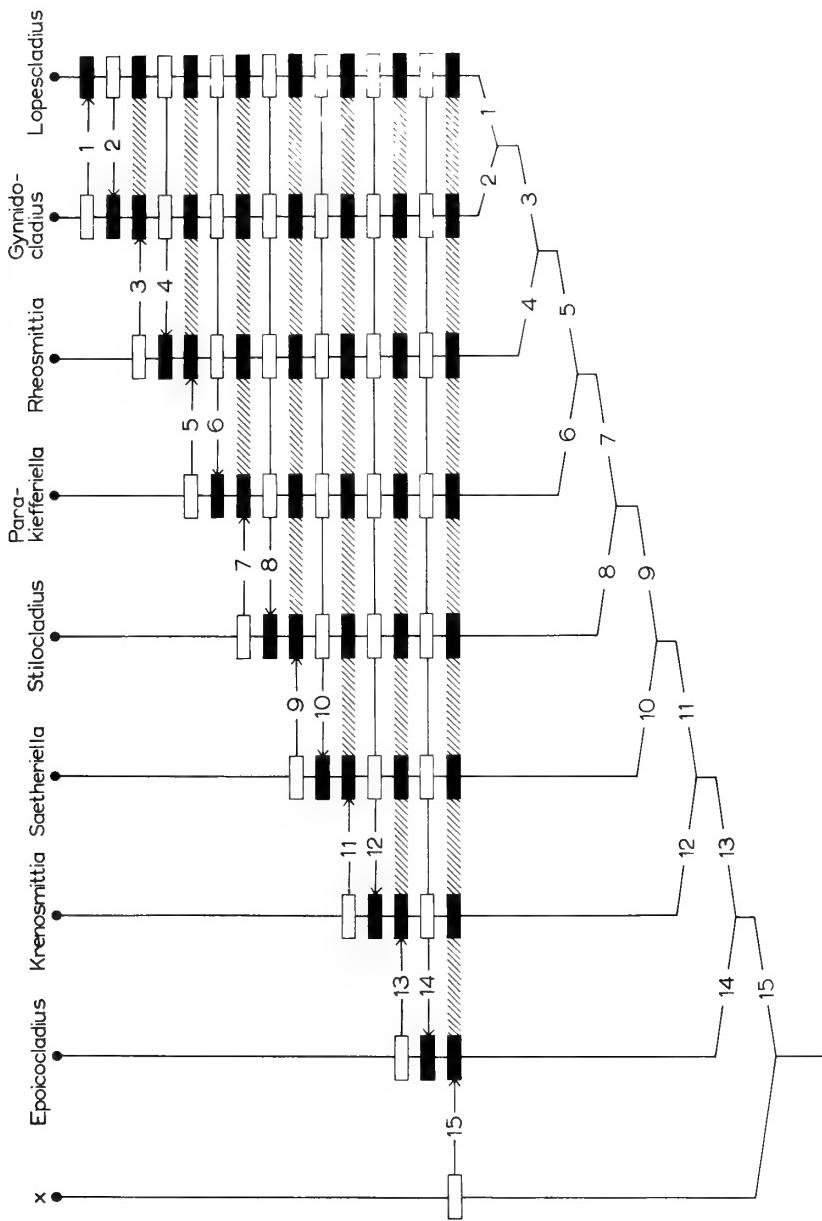
FIG. 1.   Scheme of argumentation delineating the cladogenesis of the *Parakiefferiella* group by means of trends 1-15.

last genus, the part of Europe which was part of Gondwanaland , indicate a Gondwanian origin of most of the group.

KEY TO KNOWN MALES OF LOPESCLADIUS OLIVEIRA

1. Gonocoxite without caudal extension; inferior volsella broadly digitiform . . . .
    . . . . *Lopescladius* n. subgen. n. sp. (Coffman & Roback in prep.)
    Gonocoxite with caudal extension; inferior volsella spiniform or absent . . . .
    . . . . *Lopescladius s. str.* 2
2. Antenna with 11 flagellomeres, AR about 1.1; inferior volsella tapering to sharp point,
    bare (Fig. 2D); extension of gonocoxite without broad apical seta . . . .
    . . . . :. . .*Lopescladius fittkaui* n. sp.
    Antenna with 13 flagellomeres, AR higher than 1.2 or lower than 0.8; inferior volsella with
    a parallelsided base, median seta, and a tapering apex (Fig. 2E) or absent; extension
    of gonocoxite with or without a broad apical seta 3
3. AR about 0.75; inferior volsella and broad seta of gonocoxite extension present (Fig. 2E)
    . . . .*Lopescladius verruculosus* n.sp.
    AR higher than 1.2 or lower than 0.6; inferior volsella and broad seta of gonocoxite exten-
    sion absent (Fig. 5; Oliveira 1967 fig. 3) 4
4. AR about 1.3 . . . . *Lopescladius minutissimus* Oliveira (Oliveira 1967 fig. 3)
    AR about 0.5 . . . . *Lopescladius inermis* n. sp.

KEY TO KNOWN PUPAE OF LOPESCLADIUS OLIVERIA

1. Spinules of anterior shagreen bands on tergites and sternites strong, spine-like; anal lobe
    projection rugulose, about equally wide in the middle as at base, about 2.3 times as
    long as wide; total length about 2.4 mm . . . .
    . . . . *Lopescladius* n. gen. n. sp. (Coffman & Roback in prep.)
    Spinules of anterior shagreen bands not conspicuously strong; anal lobe projection smooth
    or when rugulose pupa more than 3.0 mm long, projection widest at base, about 2.6
    times as long as wide; total length 1.3-2.1 mm or 3.0-3.3 mm . . . .
    . . . . *Lopescladius s. str.* 2
2. Exuvia dark brown; total length 3.0-3.3 mm; anal lobe projection very distinctly rugulose
    (Fig. 6F). . . . . *Lopescladius* sp. *F*
    Exuvia pale yellowish to greyish brown; total length 1.3-2.1 mm; anal lobe projection
    smooth to slightly rugulose 3
3. Extensive rugulosity extends onto frontal apotome, antennal and wing sheaths (Fig. 4A, B)
    4
    Rugulosity well developed, but frontal apotome, antennal and wing sheaths smooth or
    at most slightly wrinkled or rugulose (Fig. 3A). 5
4. Lateral rugulosity of abdominal segments extending for most of the length of each seg-
    ment (Fig. 4D), digitiform projections of anal lobe 90-113 μm long and about 2.8
    times as long as basally wide . . . . *Lopescladius verruculosus* n.sp.
    Lateral rugulosity of abdominal segments restricted to medial half (Fig. 4E); digitiform
    projections of anal lobe 75-83 μm long and about 3.4-3.7 times as long as basally
    wide . . . . *Lopescladius* sp. *E*
5. Tergite I with more than 2 posterior spines (Fig. 6A, B) 6
    Tergite I usually without, at most with 2 weak, posterior spines (Fig. 3D) 8

6.   Anal lobe projection slightly wrinkled (Fig. 6E) to distinctly rugulose medially (Fig. 6D) or near apex, 109-135 μm long and 1.2-1.4 times as long as anal macrosetae; exuvia greyish brown 7
    Anal lobe projection nearly smooth, 86-101 μm long and 0.9-1.1 times as long as anal macrosetae; exuvium very pale yellowish . . . . *Lopescladius* sp. A
7.   Anal lobe projection distinctly rugulose medially (Fig. 6D) 120-135 μm long, about 3.6-4.1 times as long as basally wide . . . . *Lopescladius* sp. C
    Anal lobe projection slightly wrinkled but not rugulose (Fig. 6E) 109-116 μm long, about 2.9-3.1 times as long as basally wide . . . . *Lopescladius* sp. D
8.   Exuvium very pale greyish yellow including cephalothorax; anterior spinules in shagrenation of segments very sparse, present mostly only anteriolaterally . . . .
    . . . . *Lopescladius* sp. B
    Exuvium with brown cephalothorax and pale greyish brown abdomen; anterior spinule bands weak but nearly complete (Fig. 3D) . . . . *L. fittkaui* n. sp.

Lopescladius fittkaui n. sp.

Type locality: Brazil, Amazonas, near Manaus, Reserva Duke.

Type Material: Holotype, male, light trap, Upper Rio Marauia, Estado Amazonas, Missionstation Sao Antonio, Brazil, 9/1/1963, E.J. Fittkau, in the collection of Zoologisches Staatssammlung, Munich, West Germany (ZSM, number on slide A 473). Paratypes, male, as holotype, drift, undisturbed forest, Igarapé Barro Branco, Reserva Duke, near Manaus, Estado Amazonas, Brazil, mature male pupa, 11 pupal exuvia 8-10/5/1961, E.J. Fittkau, A 174-1; 1 exuvium, as above except 2/2/1961, A 116-1 (ZSM, ZMBN).

Diagnostic characters: See key on p. 286.

Etymology: Named in honour of Dr. E.J. Fittkau, Zoologisches Staatssammlung, Munich, the collector of two of the new species described here.

Male imago   (n = 2 except when otherwise stated)
Total length about 1.3 mm (1). Wing length 0.58-0.60 mm. Total length/wing length about 2.2 (1). Wing length/length of profemur 3.33-3.44. Coloration yellowish brown.

Head (Fig. 2A). Antenna with 11 flagellomeres, ultimate flagellomere 131 μm (1) long, AR 1.09 (1). Clypeus with 2 setae. Cibarial pump, tentorium and stipes as in Fig. 2A. Tentorium 56 μm (1) long, 7 μm (1) wide. Palp lengths/(micrometers, n = 1): 8, 9, 17, 32, 45.

Thorax (Fig. 2B). Antepronotum with 1 lateral seta. Dorsocentrals apparently 3-4, prealars 2. Scutellum with 2 setae.

Wing (Fig. 2C). VR 1.51-1.56.

Legs.   Spur of front tibia 19 μm long, spurs of middle tibia 15μm and absent, of hind tibia 26μm and 8-9 μm. Width at apex of front tibia 17-18 μm, of middle tibia 15 μm, of hind tibia 20 μm. Comb with 7-8 setae, 11-17 μm long. Lengths (micrometers) and proportions of legs:
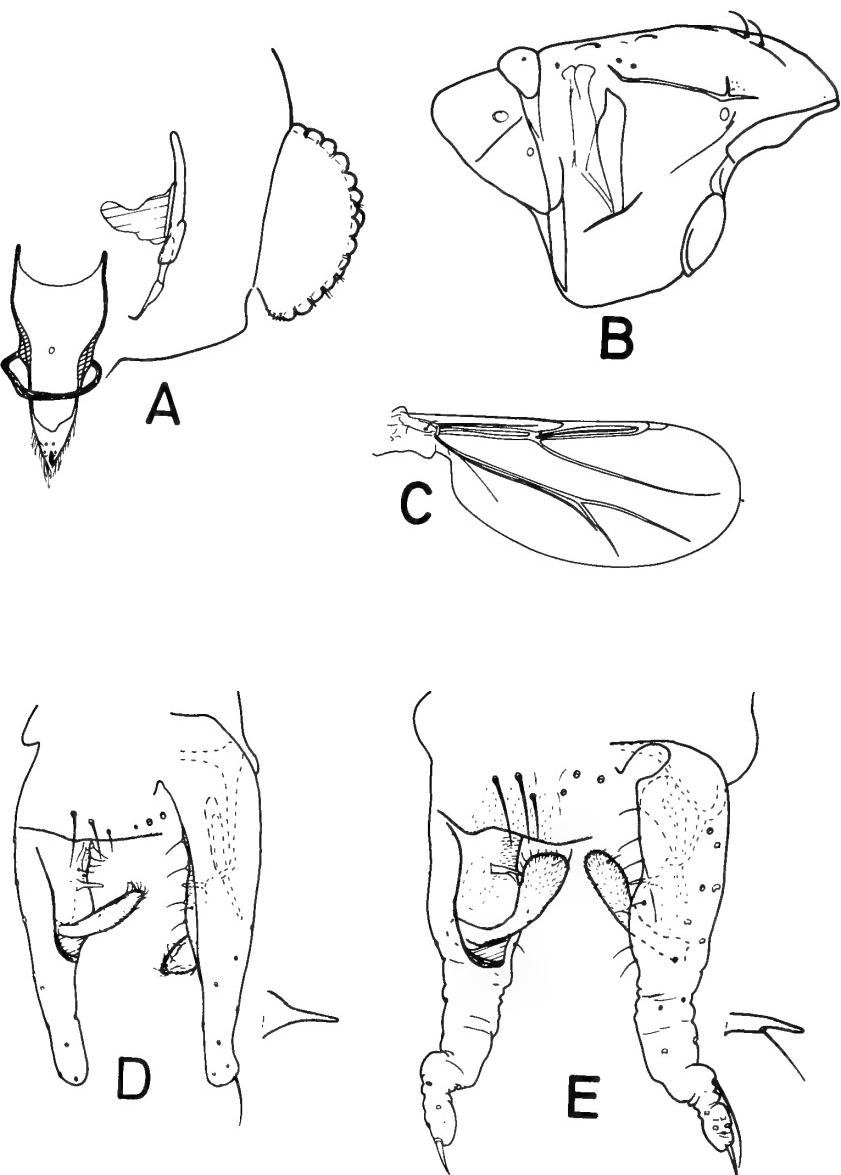
FIG. 2. *Lopescladius* spp., male. — A-D. *L. fittkaui* n. sp. — A. Eye, cibarial pump, tentorium and stipes. — B. Thorax. — C. Wing. — D. Hypoygium — E. *L. verruculosus,* hypopygium.

	fe	ti	ta$_1$	ta$_2$	ta$_3$	ta$_4$	ta$_5$
p$_1$	173	188-203	75-79	41	30	11	23
p$_2$	225-236	236-249	83-84	34	23	11	19-21
p$_3$	176-184	227-240	69-73	32-34	23-26	9-11	19-21

	LR	BV	SV	BR
p$_1$	0.39-0.40	4.14-4.32	4.76-4.80	1.7-1.8
p$_2$	0.34-0.35	6.17-6.61	5.50-5.76	2.3
p$_3$	0.31-0.34	5.52-5.60	5.79-5.80	1.9-2.0

Hypopygium (Fig. 2D). Tergum IX with 4-6, 5 (3) setae; laterosternite IX apparently bare. Apodemes not measurable. Gonocoxite 143μm (3) long, distance from base to base of gonostylus 79-83μm; inferior volsella tapering, bare, 10-13μm long, 4-5μm wide at base, 1.5μm side one third from base. Gonostylus 38-41, 39μm (3) long. HR 3.45-3.80, 3.68 (3); HV about 3.2.

Pupa (n = 10 except when otherwise stated)

Total length 1.51-1.86, 1.65 mm. Thorax of exuvia brown, abdomen pale greyish brown.

Cephalothorax (Fig. 3A-C). Frontal apotome (Fig. 3A), antennal sheath and wing sheath smooth. Postorbital 19-23, 22μm (3) long. Median antepronotal setae 41-49, 43μm (8) and 30-49, 37μm (8) long; lateral antepronotals 38-41, 38μm (9) and 4-11, 6μm (8) long. Posterior precorneal seta (Fig. 3A) 38-45, 40μm (8) long; median and anterior both 26-38, 32μm long. Anterior two dorsocentrals (Dc$_1$, Dc$_2$) both 26-45, 39μm (9) long; Dc$_3$ 8-26, 15μm (8) long; Dc$_4$ 15-38, 26μm (8) long. Distance between Dc$_1$ and Dc$_2$ 11-21, 15μm; between Dc$_2$ and Dc$_3$ 88-116, 100μm; between Dc$_3$ and Dc$_4$ 9-34, 22μm.

Abdomen (Fig. 3D-G). Shagrenation and chaetotaxy as in Figs. 3D-G and generic diagnosis. Number of caudal spines on tergites I-VIII as: 0-2, 0; 9-15, 12; 10-14, 11; 9-13, 11; 9-12, 11; 8-13, 10; 8-14, 10; 6-10, 8. Number of caudal spines on sternites II-VIII as: 4-7, 5; 8-11, 9; 7-11, 9; 7-11, 9; 7-10, 9; 6-10, 8; 0 (6 ♀♀), 5-9, 8 (4 ♂♂). Digitiform projection of anal lobe smooth, about 2.8 times as long as wide, 86-101, 94μm long. Anal macrosetae 83-101, 92μm long.

Larva. Unknown.

Lopescladius verruculosus n. so.

Type locality: Mexico, Prov. Michoacan, river mouth about 100 km south of Tocuman.

Type material: Holotype, male, river mouth about 100 km south of Tocuman, prov. Michocan, Mexico, April 1981, E.J. Fittkau, in the collection of Zoologisches Staatssammlung, Munich, West Germany (ZSM). *Paratypes,* 60 pupal exuvia, as holotype. *Other material:* pupa, Mississippi River, near Cordoba, Illinois, 13/9/72, D.L. Andersen (ZSM, ZMBN).

Diagnostic characters: See key on p. 286.
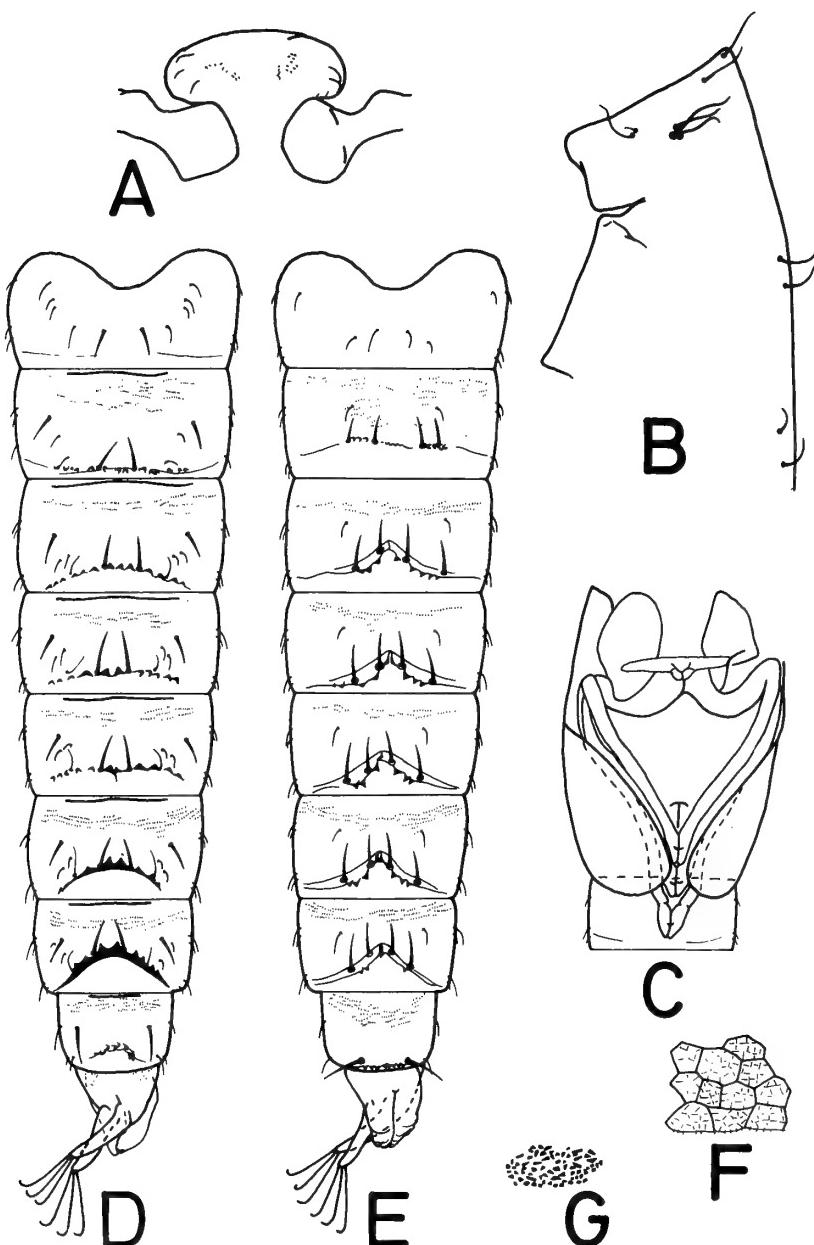
Etymology: From Latin *verruculosus,* full of small warts, referring to the rugulosity which extends onto the frontal apotome and the antennal and wing sheaths of the pupa.

Male imago (n = 1)
Total length about 1.4 mm. Wing length about 0.6 mm. Total length/wing length about 2.2 mm. Wing length/length of profemur about 3.3 mm. Coloration yellow brown.

Head. Antenna with 13 flagellomeres, ultimate flagellomere 128μm long, AR 0.74. Palpal segments 4 and 5 respectively 36μm and 60μm long. Other details of head not measurable.

Thorax. Antepronotum apparently bare. Dorsocentrals apparently 2-3, prealars 2. Scutellum with 2 setae.

Wing. VR not measurable.

Legs. Spur of front tibia 19μm long, spurs of middle tibia 15μm and 7μm long, of hind tibia 21μm and perhaps absent. Width at apex of front and middle tibia 19μm, of hind leg 23μm. Comb with 9 setae, 11-17μm long. Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	191	221	86	49	39	15	26	0.39	3.86	4.78	2.0
p_2	248	244	90	43	34	15	24	0.37	5.00	5.46	2.5
p_3	210	244	71	34	26	15	24	0.29	5.28	6.37	2.0

Hypopygium (Fig. 2E). Tergum IX with 6 setae; laterosternite IX apparently bare. Apodemes not measurable. Gonocoxite 169μm long, distance from base to base of gonostylus 79μm; inferior volsella with median seta, 13μm long, 2.5μm wide and parallel-sided in basal half; 1.5μm wide about 0.6 from base and tapering to point, projection of gonocoxite with conspicuous spine-like apical seta. Gonostylus 60μm long, HR 2.81, HV about 2.4.

Pupa (n = 10)
Total length 1.56-1.94, 1.77 mm. Exuvia pale yellowish brown.

Cephalothorax Frontal apotome (Fig. 4A), antennal sheath and wing sheath covered with rugulosity. Postorbital 11-21, 17μm long. Median antepronotal setae 26-38, 32μm and 23-34, 26μm (8) long; lateral antepronotals 19-38, 29μm and 4-8, 6μm long. Anterior precorneal seta 15-34, 23μm long; median and posterior both 11-19, 14μm long. Anterior two dorsocentrals (Dc_1, Dc_2) and posterior dorsocentral (Dc_4) all 15-16, 20μm long, Dc_3 11-19, 14μm long. Distance between Dc_1 and Dc_2 11-23, 16μm; between Dc_2 and Dc_3 90-124, 106μm; between Dc_3 and Dc_4 6-38, 14μm.

Abdomen (Fig. 4C-D). Shagrenation and chaetotaxy as in Fig. 4C-D and generic diagnosis. Number of caudal spines on tergites II-VIII as: 8-16, 12; 9-16, 12; 9-12, 11; 10-13, 11; 9-11, 10; 6-10, 8; 2-9, 7. Number of caudal spines on sternites II-VIII as: 4-9, 6; 8-13, 10; 8-12, 10: 7-12, 9; 6-10, 8; 6-8, 7; 0 (♀ ♀), 4-7, 5 (♂ ♂). Digitiform projection of anal lobe smooth, about 2.8 times as long as basally wide, 90-113, 102μm long. Anal macrosetae 90-116, 103μm long.

Larva. Not known with certainty.

FIG. 3. *Lopescladius fittkaui* n. sp., pupa. — A. Frontal apotome. — B. Chaetotaxy of cephalothorax. — C. Leg sheath arrangement. — D. Tergites. — E. Sternites. — F. Reticulation and spinules of tergites. — G. Polygones of conjunctives.
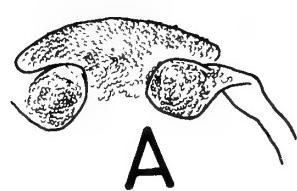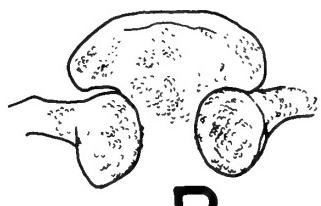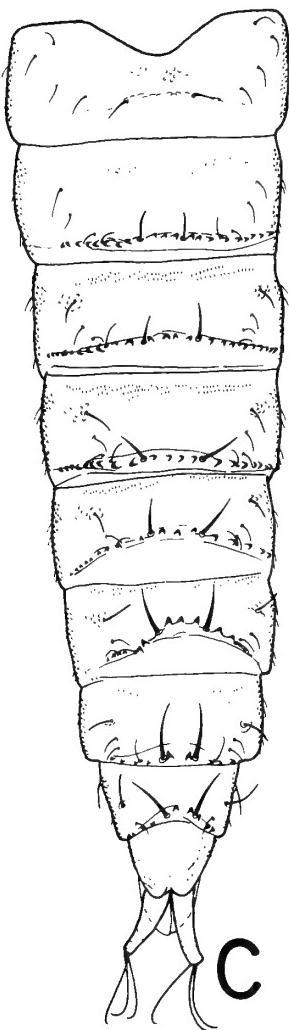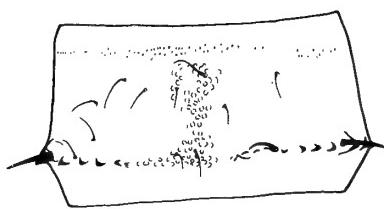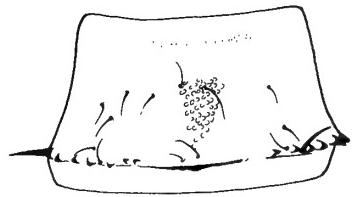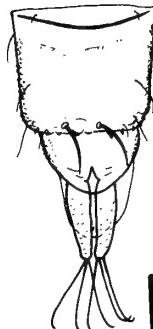
Lopescladius inermis n. sp.

Type locality: U.S.A., Kansas, Meade Co., near Meade Co. State Lake.

Type material: Holotype, male, artesian spring at Meade Co. State Lake, Meade Co., Kansas, U.S.A., 16/7/80, P. Liechti & M. Orbois, in the collection of Museum of Zoology, University of Bergen (ZMBN No. 73).

Diagnostic characters: See key on p. 286.

Etymology: From Latin *inermis* meaning unarmed referring to the lack of a spine-like inferior volsella.

Male imago Total length about 1.59 mm. Wing length 0.73 mm. Total length/wing length 2.18. Wing length/length of profemur 3.24. Coloration yellowish brown with darker vittae, postnotum and lower parts of preepisternum.

Head. Antenna with 13 flagellomeres, ultimate flagellomere 137μm long, AR 0.51. Temporal setae absent except for 1 weak postorbital. Clypeus with 2 setae. Cibarial pump, tentorium and stipes as in Fig. 5A. Tentorium 71μm long, 7μm wide. Stipes 77μm long. Palp lengths (micrometers): 11, 15, 21, 30, 58.

Thorax (Fig. 5B). Antepronotum with 1 lateral seta. Dorsocentrals 4, prealars 2. Scutellum with 2 setae.

Wing (Fig. 5C). VR 1.42. Brachiolum with 1 seta, other veins bare.

Legs. Spurs of front tibia 21μm long, spurs of middle tibia 17μm and absent, of hind tibia 41μm and 15μm. Width at apex of front tibia 21μm, of middle tibia 19μm, of hind tibia 26μm. Comb with 11 setae, 9-17μm long. Lengths (micrometers) and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BV	SV	BR
p_1	225	255	90	51	41	13	28	0.35	4.28	5.33	2.2
p_2	244	313	90	41	32	11	26	0.29	5.85	6.19	3.0
p_3	233	302	86	38	30	11	28	0.29	5.81	6.20	2.5

Hypopygium (Fig. 5C). Tergum IX with 7 setae, laterosternite IX apparently bare. Phallapodeme strongly developed, 99μm long, with large aedeagal lobe. Transverse sternapodeme broadly rounded without oral projections. Gonocoxite 180μm long, distance from base to base of gonostylus 116μm; inferior volsella absent, perhaps represented by a weak seta. Gonostylus 57μm long. HR 3.16, HV 2.79.

Remarks. The species appear intermediate between *Lopescladius minutissimus* and *L. fittkaui*. The hypopygium is lacking an inferior volsella as apparently also *L. minutissimus* does, while the hypopygium otherwise is very similar to that of *L. fittkaui*. Also while the antenna has 13

FIG. 4. *Lopescladius* spp., pupae. — A. *Lopescladius verruculosus,* frontal apotome and antennal sheath base. — B. *Lopescladius* sp. *E,* frontal apotome, C-D. *Lopescladius verruculosus.* — C. Abdomen. — D. Lateral view of segment IV. — E-F. *Lopescladius* sp. *E.* — E. Lateral view of segment IV. — F. Tergites VIII-IX and anal lobe.
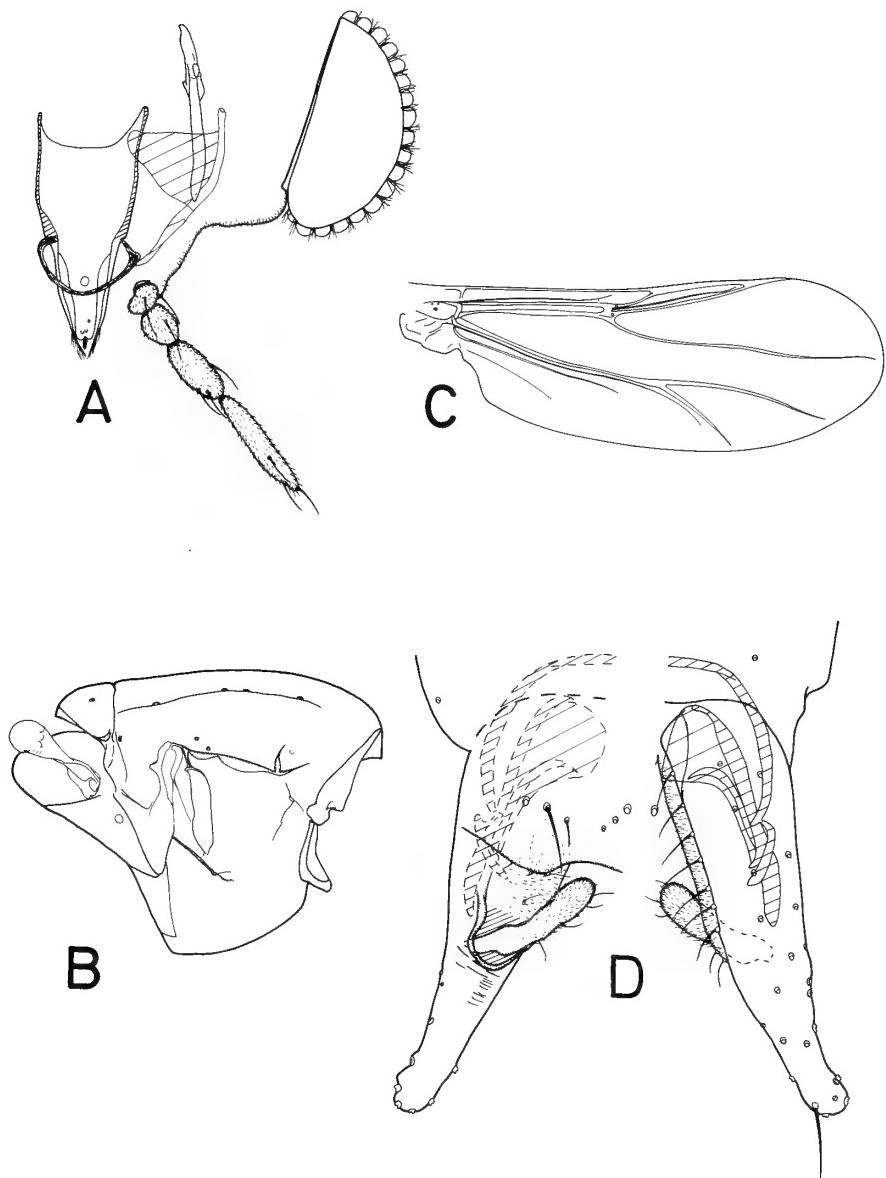
FIG. 5.   *Lopescladius inermis* n. sp., male. — A. Eye, cibarial pump, tentorium and stipes. — B. Thorax. — C. Wing. — D. Hypopygium.

flagellomeres the AR is lower than in *L. minutissimus* and *L. verruculosus*. Unfortunately *L. minutissimus* could not be reexamined. However, judging on the figures the hypopygium appears similar to *L. verruculosus* and these two species combined could well form the sister group of *L. inermis* and *L. fittkaui* combined.

Lopescladius sp. A (Fig. 6A)

These exuvia have a pale yellowish coloration, 3-6 spines on tergite I (Fig. 5A) and a size of 1.7-2.0 mm. All other details appear identical to those of *L. fittkaui* n. sp.

Material examined: 29 pupal exuvia, left tributary to River Huallago at Huanoco, 1 900 m.a.s.l., Peru, 1963, E.J. Fittkau; 18 pupal exuvia, tributary Rio Chaohamayo at San Ramon, 1 700 m.a.s.l., Peru, 15/5/63, E.J. Fittkau.

Lopescladius sp. B (Fig. 6B, C)

These exuvia have a very pale greyish yellowish coloration including the cephalothorax, no caudal spines on tergite I, and a length of 1.31-1.56 mm. The anterior shagreen of the abdomen consists mostly of a few anteriolateral spinules only. Except for details connected with the smaller size the exuvia otherwise are very similar to these of *L. fittkaui* n. sp. and could conceivably be a form of that species.

Material examined: 94 exuvia, drift, Rio Negro, 2 km below Tapunquara, Brazil, 6/2/63, E.J. Fittkau.

Lopescladius sp. C (Fig. 6D)

These exuvia have the digitiform anal lobe projection rugulose particularly medially. The frontal apotome also is weakly rugulose medially, while there is some slight rugulosity at base of the antennal sheaths. The size is about 2.0 mm, the digitiform anal lobe projections are 120-135μm, about 3.6-4.1 times as long as basally wide and about 1.3-1.4 times as long as the anal macrosetae. There are several caudal spines present on tergite I and the anterior transverse rows of spinules in the group shagreen are nearly complete.

Material examined: 4 exuvia, drift, Rio Marauia, Brazil, 28/1/63, E.J. Fittkau.

Lopescladius sp. D (Fig. 6E)

These exuvia have the digitiform anal lobe projection slightly wrinkled, but not rugulose. The projection is 109-116μm long, about 2.9-3.1 times as long as basally wide, and about 1.2-1.3 times as long as the anal macrosetae. The length of the exuvia are 1.81-1.95 mm and the coloration greyish brown. The frontal apotome, antennal and wing sheath are nearly smooth. Tergite I has about 6 caudal spines and the spinules in the anterior group shagreen are placed in a nearly continuous line.

The species appear close to *Lopescladius* sp. **C.**
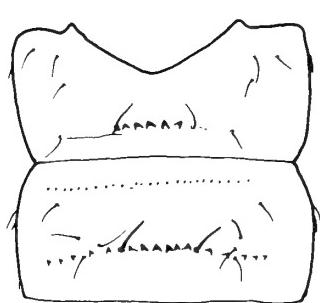
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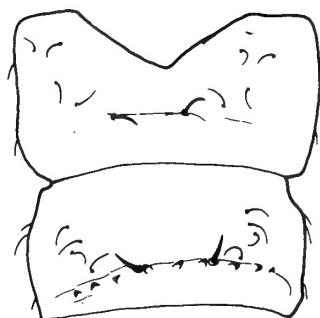
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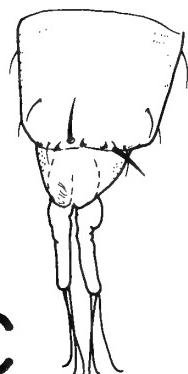
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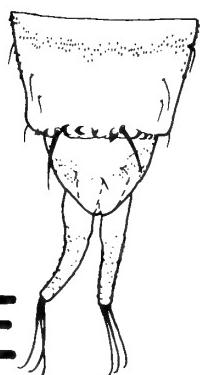
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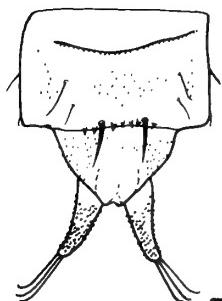
F

Material examined: 17 exuvia, Panguana, Peru, 3° 37'S, 74° 56'W, ca. 260 m a.s.l. 3/4/82, E.J. Fittkau.

Lopescladius sp. E (Fig. 4B, E-F)

These exuvia have a pale yellowish brown coloration, a length of 1.43-1.52 mm; the digitiform projections are smooth, about 75-83μm long, and about 3.4-3.7 times as long as basally wide; and the anal macrosetae are 71-81μm long. They resemble *L. verruculosus* n. sp. in having the frontal apotome, antennal sheath and wing sheath covered with rugulosity. The rugulosity particularly of the frontal apotome (Fig. 4B) is weaker and while the tergites in *L. verruculosus* have a strong lateral rugulosity extending for most of the length of each segment (Fig. 4D), the lateral rugulosity of *Lopescladius* sp. *E.* is restricted to the median half (Fig. 4E).

The species could be a form of *L. verruculosus.*

Material examined: 23 exuvia, drift, Rio Tocantus near Baiao, Brazil, 28/10/1960, E.J. Fittkau.

Lopescladius sp. F (Fig. 6F)

These exuvia have a dark brown coloration, a size of 3.0-3.4 mm, the digitiform projections are distinctly rugulose (Fig. 5F) and about 150-160μm long, tergite I have a few caudal spines, the frontal apotome is weakly and partly rugulose, the antennal sheaths are smooth, the wing sheath have some rugulosity near apex, and the posterior bands of anterior spinules on the tergites are placed on a continuous transverse line.

Material examined: 5 exuvia, drift, middle part of Rio Prete da Eva, Estado Amazonas, Brazil, 14/10/1965, E.J. Fittkau.

FIG. 6. *Lopescladius* spp., pupae. — A. *Lopescladius* sp. *A,* tergites I-II. — B. *Lopescladius* sp. *B,* tergites I-II. — C-F. Tergites VIII-IX and anal lobe. — C. *Lopescladius* sp. *B.* — D. *Lopescladius* sp. *C.* — E. *Lopescladius* sp. *D.* — F. *Lopescladius* sp. *F.*

REFERENCES

BRUNDIN, L. 1956. Zur Systematik der Orthocladiinae (Dipt., Chironomidae). — Rep. Inst. Freshwat. Res. Drottningholm 37:5-185.

_____. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. With a monograph of the subfamilies Podonominae and Aphroteniinae and austral Heptagyiae. — K. Svenska VetenskAkad. Handl. 11:1-472.

COFFMAN, W.P. AND S.S. ROBACK. [in preparation]

CRANSTON, P.S., D.R. OLIVER AND O.A. SAETHER. 1982. Orthocladiinae. In Wiederholm, T. (ed.): Chironomidae of the Holarctic region. Part 1. Larvae. — Ent. scand. Suppl.

CRANSTON P.S. AND O.A. SAETHER. A revision of European *Rheosmittia* Brundin [in MS].

HALVORSEN, G.A. 1982. *Saetheriella amplicristata* gen. n., sp. n., a new Orthocladiinae (Diptera: Chironomidae) from Tennessee. Aquatic Insects 4:131-136.

ROBACK, S.S. 1953. Savannah River tendipedid larva (Diptera: Tendipedidae — Chironomidae). — Proc. Acad. Nat. Sci. Philad. 105:91-132.

SAETHER, O.A. 1979. Underlying synapomorphies and anagenetic analysis. — Zool. Ser. 8:305-312.

_____. 1980. Glossary of chironomid morphology terminology (Diptera: Chironomidae). — Ent. scand. Suppl. 14:1-51.

_____. 1981. Orthocladinae (Chironomidae: Diptera) from British West Indies, with descriptions of *Antillocladius* n. gen., *Lipurometriocnemus* n. gen., *Compterosmittia* n. gen., and *Diplosmittia* n. gen. — Ent. scand. Suppl. 16:1-46.

_____. 1982. Orthocladinae (Diptera: Chironomidae) from SE U.S.A., with descriptions of *Plhudsonia, Unniella, Platysmittia* n. genera and *Atelopodella* n. subgen. — Ent. scand. 13:465-510.

SAETHER, O.A. AND G.A. HALVORSEN. 1981. Diagnoses of *Tvetenia* Kieff., emend., *Dratnalia* n. gen., and *Eukiefferiella* Thien., emend., with a phylogeny of the *Cardiocladius* group (Diptera: Chironomidae). — Ent. scand. Suppl. 15:269-285.

SAETHER O.A. AND J.E. SUBLETTE. 1983. A review of the genera *Doithrix* n. gen. *Georthocladius* Strenzke, *Parachaetocladius* Wülker, and *Pseudorthocladius* Goetghebuer (Diptera: Chironomidae, Orthocladiinae). — Ent. scand. Suppl. 20 [in press].

SUBLETTE, J.E. AND W.W. WIRTH. 1980. The Chironomidae and Ceratopogenidae (Diptera) of New Zealand's subantarctic islands. — N.Z.Y. Zool. 7:299-378.

Wing Character Variation in the Nearctic species of Orthocladius (Orthocladius) van der Wulp (Diptera: Chironomidae): a Principal Components Analysis

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ABSTRACT. — Variation in eight characters, wing length, wing width, distance from arculus to crossvein rm, distance from arculus to fork of the cubitus, the numbers of radial and squamal setae, thorax length, and abdomen length, was investigated in males of 22 species of *Orthocladius (Orthocladius)* using principal components analysis. The first 3 principal components (PC) accounted for 96-98 percent of the observed variation: PC1, a general size factor, accounted for 77-83 percent; PC2, which largely corresponds to variation in radial setae number, accounted for 10-15 percent; and PC3, which contrasts squamal setae number with wing size, accounted for 3-5 percent. Within males of *O. (Orthocladius)*, the number of radial setae and thorax length display negative allometry, while the number of squamal setae displays positive allometry with respect to size. This analysis suggests that wing length may be used as a reliable index of size, and that the numbers of radial and squamal setae may prove useful for separating species or species groups within genera of the Orthocladiinae.

INTRODUCTION

The Nearctic species of the subgenus *Orthocladius (Orthocladius)* van der Wulp were recently revised by Soponis (1977). Species recognition within *Orthocladius* and many other chironomid genera is based primarily on the genitalic structure of adult males, e.g., Townes 1945, Brundin 1956. However, descriptions of chironomids are among the most quantitative of all zoological descriptions and generally include detailed data on various lengths and counts, e.g., Oliver 1977, Saether 1977. Even though selected quantitative characters have been used to separate species (Saether 1976), much of the available data has gone unanalyzed.

The objective of this study was to evaluate wing character variation in males of *O. (Orthocladius)* through the use of principal components analysis (PCA). Thorax and abdomen lengths were also included in the analysis to facilitate the evaluation of size effects. Twenty-two of the 29 Nearctic species recognized by Soponis (1977) were represented by sample sizes sufficiently large to allow analysis.
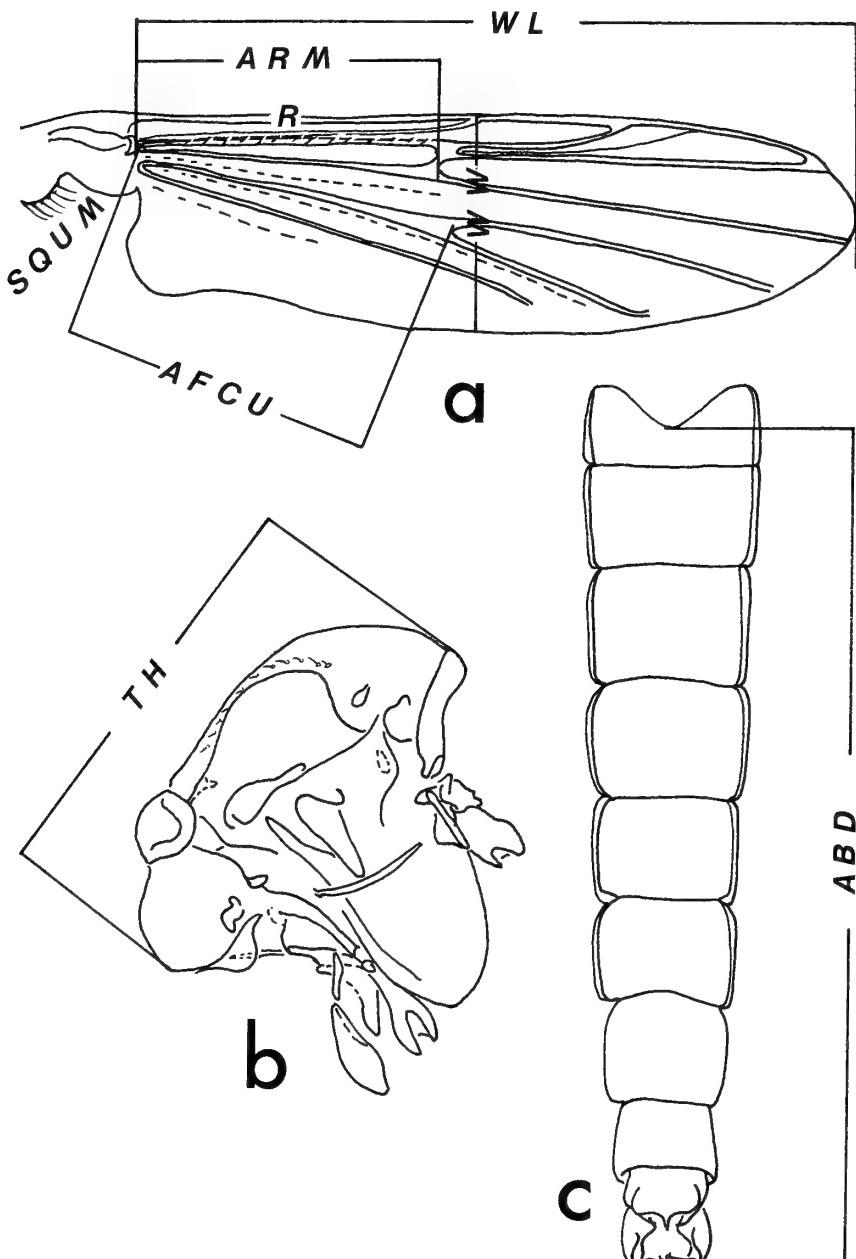
FIG. 1. Wing (a), thorax (b), and abdomen (c) of male of *Orthocladius* showing measurements and setae with character abbreviations: WL - wing length; ARM - distance from arculus to crossvein rm; AFCU - distance from arculus to fork of the cubitus; WW - wing width; R - number of setae on vein R; SQUM - number of setae on squama; TH - thorax length; ABD - abdomen length.

METHODS

Definitions and abbreviations for characters treated herein are provided in the legend of Fig. 1. Species studied are numbered and alphabetically listed in the legend for Fig. 2: the corresponding numbers from Fig. 2 are employed in lieu of names in all ordinations (Figs. 2-4).

One to 3 sets of character values were selected for each species. For each species, 1 set consisted of the mean values for all specimens studied by Soponis (1977). Additionally, for each species the largest and smallest specimens for which reliable data on all 8 characters were available were included. The mean value and sample size for each species are provided by Soponis (1977), and data on the largest and smallest specimens are available from the authors. Complete data sets for large specimens of *O. dentifer* Brundin and *O. robacki* Soponis, and small and large specimens of *O. trigonolabis* Edwards were unavailable.

PCA on the correlation matrix of standardized characters (Table 1) and variance-covariance matrix of the log transformed data (Table 2), followed by ordination on the first 3 principal components from the correlation matrix were employed to reduce the dimensionality of the data and to examine relationships among selected body length and wing characters. For n characters, PCA produces n linear combinations of the original characters, or n principal components (PC), such that the first PC is the longest axis of the concentration ellipsoid of the multivariate normal density function in the n-dimensional character space for the taxa being investigated. Thus, PC1 is the linear combination of characters that explains the largest portion of the variation in the data. The second PC is defined to be that linear combination of the original characters that explains the second largest amount of variation, subject to the restraint that PC2 be uncorrelated, or orthogonal to PC1. Subsequent PCs are defined in a similar fashion. Each PC is characterized by 1 eigenvalue and n coefficients, or 1 coefficient for each character (Pimentel 1979). The relative size of an eigenvalue corresponds to the percent of the total variance explained by that PC (Tables 1-2). Each coefficient represents the direction of variance for 1 character on the associated PC. Interpretation of PCs is facilitated by the use of a correlation coefficient between each character and PC (Tables 1-2).

The use of 3 PC scores for each species allows for assessment of species variation and the effects of size within a species (Figs. 2-4). However, the size and position of the triangle for each species is highly dependent upon the selection of the large and small specimens, and provides only a rough approximation of the size and position of the ellipse of species variation. In addition, triangles for species represented by small sample sizes, particularly *O. knuthi* Soponis (11, Figs. 2-4) and *O. wiensi* Saether (22, Figs. 2-4), provide poor estimates of the true species ellipse.
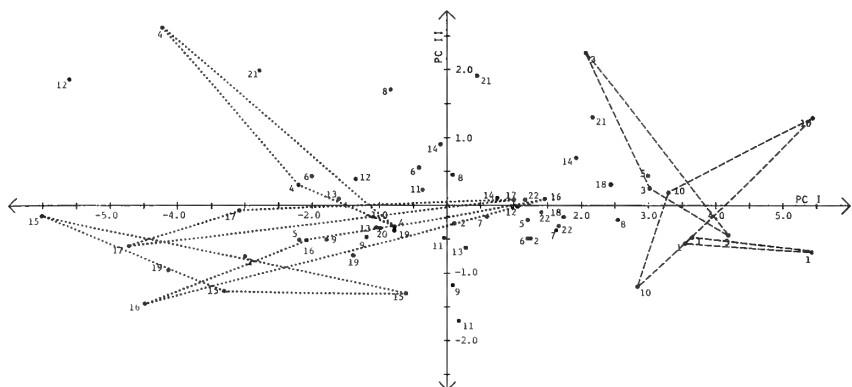
FIG. 2. Males of 22 species of *O. (Orthocladius)*. Ordination by principal components analysis of standardized character correlations, component 1 vs. 2. Dots connect values for 4 large species (4, 15, 16, 17); dashes connect values for 3 small species (1, 3, 10). Species are listed alphabetically and numbered as follows: 1 — *annectens* Saether; 2 - *appersoni* Soponis; 3 - *carlatus* (Roback); 4 - *charensis* Soponis; 5 - *clarkei* Soponis; 6 - *decoratus* (Holmgren); 7 -*dentifer* Brundin; 8 - *dorenus* (Roback); 9 - *hazenensis* Soponis; 10 - *hellenthali* Soponis; 11 -*knuthi* Soponis; 12 - *lapponicus* Goetghebuer; 13 - *mallochi* Kieffer; 14 - *manitobensis* Saether; 15 - *nigritus* Malloch; 16 - *obumbratus* Johannsen; 17 - *oliveri* Soponis; 18 - *robacki* Soponis; 19 - *subletti* Soponis; 20 - *trigonolabis* Edwards; 21 - *tryoni* Soponis; 22 - *wiensi* Saether.
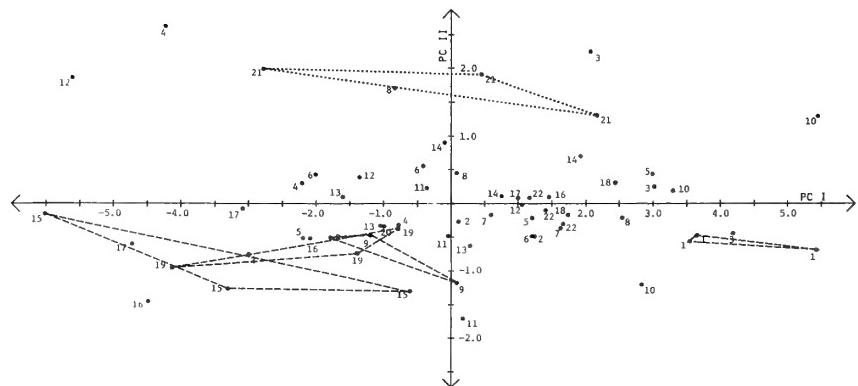
FIG. 3. Males of 22 species of *O. (Orthocladius)*. Ordination by principal components analysis of standardized character correlations, component 1 vs. 2. Dots connect values for a species with large PC2 scores (21); dashes connect values of 4 species with small PC2 scores (1, 9, 15, 19). Species are numbered as in Fig. 2.
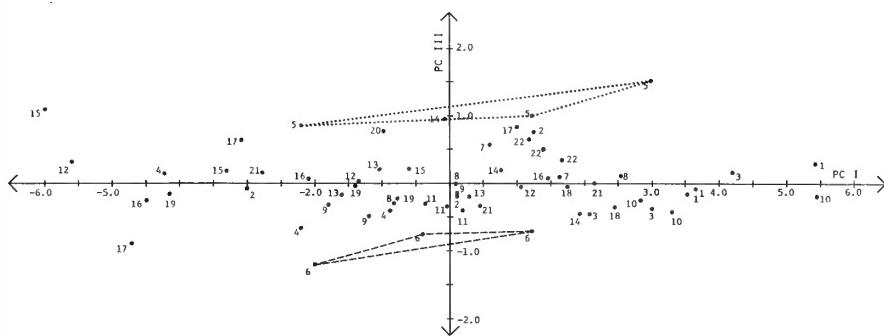
FIG. 4. Males of 22 species of *O. (Orthocladius)*. Ordination by principal components analysis of standardized character correlations, component 1 vs. 3. Dots connect values for a species with large PC3 scores (5); dashes connect values for a species with small PC3 scores (6). Species are numbered as in Fig. 2.

Conclusions drawn from Anderson's (1963) test of multivariate isometry and Jolicoeur's (1963a, 1963b) paired comparison method were verified by regression analyses employing Hotelling's T^2 and Bonferroni confidence intervals, and by separate PCA on selected data subsets. For example, separate PCA were conducted on the 6 length characters, and on the 4 wing size and vein length characters.

Recently, several biostatisticians (Mosimann 1970, Sprent 1972, Humphries et al. 1981) have criticized the labelling of PC1, or the first general factor, as a size factor and the labelling of subsequent bipolor components as shape factors. These authors point out that size and shape are not completely dissociated by PCA and that each PC will contain both size and shape components (Humphries et al. 1981). Although this argument is valid, see discussion of PC2 and PC3, labelling PC1 as a general size factor may be beneficial if the vast majority of the variation explained by the PC is directly related to size. Within males of *O. (Orthocladius),* PC1 and each of the 6 length variables are very highly correlated (r > .94). Thus, labelling PC1 as a general size factor facilitates dimension reduction and interpretation of the data; even though, PC1 may contain a small shape component, and subsequent PCs may contain size components. The argument against labelling subsequent bipolor components as shape variables is more appropriate as these components are generally more homogeneous mixtures of size and shape. Herein, subsequent components are treated as contrast between particular groups of characters.

RESULTS AND DISCUSSION

PCA on the correlation matrix of the standardized data (Table 1) and on the variance-covariance matrix of the log transformed data (Table 2) produced similar results. Differences in the percentage of variation explained by each PC for the 2 procedures (Tables 1-2) largely result from the larger variances of the radial and squamal setae characters. However, the correlation coefficients between each character and PC (Tables 1-2) are generally of the same magnitude and sign and similar interpretations may be drawn from each procedure.

The first 3 PCs account for 96-98 percent of the variation in the 8 characters surveyed. The first PC accounts for the vast majority of the variation in the data, between 77.36 and 82.67 percent (Tables 1-2), and appears to be most parsimoniously interpreted as a general size factor. All characters are highly correlated with PC1 (Tables 1-2) except for radial setae number, which is only weakly correlated with the other length characters and hence size. The 6 length characters, WL, ARM, AFCU, WW, TH, ABD (Fig. 1), are very highly and approximately equally correlated with PC1 (r > .94), or size.

Allometric relationships for each character with respect to size may be assessed by inspection of the coefficients for each character on PC1, the general size component, from the log transformed data (Table 2, top). Generalization of the allometry equation to the multivariate case (Anderson 1963, Jolicoeur 1963a, 1963b) allows for a test of the null hypothesis of multivariate isometry, or that all characters increase at constant rates with respect to size. For males of *0. (Orthocladius)* the multivariate isometry hypothesis may be rejected ($X^2 = 101$, n = 62, P < .005). It is apparent from the coefficients in Table 2 that all characters do not increase at a constant rate with increasing size. Characters with coefficients for PC1 roughly equal to .3535, or $1/\sqrt{n}$, display isometry, or increase at a constant rate with respect to size. Characters such as SQUM with coefficients larger than .3535 display positive allometry, or increase at increasing rates with increasing size. Characters such as R and TH with coefficients less than .3535 display negative allometry, or increase at decreasing rates with increasing size. Allometric relationships between character pairs may also be investigated by use of their PC1 coefficients (Jolicoeur 1963), although no significance test is available (Pimental 1979). Thus, SQUM displays positive allometry with respect to each of the other characters as its coefficient on PC1 is greater than that for each of the other characters, while R and TH display negative allometry with respect to the remaining wing characters and abdomen length. Regression analyses employing Hotelling's T^2 and Bonferroni confidence intervals, and separate PCA on various data subsets in-

TABLE 1. PCA on the standardized correlation matrix for males of *O. (Orthocladius)*.

| | Correlation coefficients between each character and PC1, PC2 and PC3 | | | | | | | | % variance |
	WL	ARM	AFCU	WW	R	SQUM	TH	ABD	explained
PC1	-.980	-.972	-.982	-.962	-.464	-.885	-.946	-.961	82.67
PC2	-.068	-.104	-.077	-.102	+.885	-.034	-.029	-.012	10.22
PC3	-.139	-.127	-.124	-.088	-.026	+.443	+.096	-.005	3.30

TABLE 2. PCA on variance-covariance matrix of log transformed data for males of *O. (Orthocladius)*.

| | Coefficients between each character and PC1, PC2 and PC3 | | | | | | | | % variance |
	WL	ARM	AFCU	WW	R	SQUM	TH	ABD	explained
PC1	-.338	-.358	-.326	-.320	-.253	-.539	-.272	-.346	77.36
PC2	-.068	-.095	-.079	-.105	+.964	-.190	-.045	-.038	15.21
PC3	-.315	-.293	-.283	-.214	+.052	+.806	-.041	-.184	5.06

| | Correlation coefficients between each character and PC1, PC2 and PC3 | | | | | | | | |
	WL	ARM	AFCU	WW	R	SQUM	TH	ABD	
PC1	-.961	-.962	-.964	-.951	-.509	-.925	-.943	-.953	
PC2	-.086	-.113	-.103	-.139	+.859	-.144	-.070	-.046	
PC3	-.229	-.202	-.214	-.162	+.027	+.354	-.037	-.130	

dicate that ARM displays positive allometry with respect to AFCU, while all other paired comparisons among WL, ARM, AFCU, WW and ABD appear isometric.

For taxonomic purposes it is often convenient to select 1 character to represent size for species within homogeneous genera. The representative size character, such as wing length in *O. (Orthocladius)*, should be: 1) isometric with respect to PC1, or the general size component; 2) highly correlated with PC1 and other length characters; 3) reliably measured; and 4) commonly used and reported in the literature.

The negative coefficients of PC1 (Tables 1-2) result in large component scores for small species (Figs. 2-4) such as *O. annectens* Saether (1), *O. carlatus* (Roback) (3), and *O. hellenthali* Soponis (10), and small (negative) scores for large species, such as *O. charensis* Soponis (4), *O. nigritus* Malloch (15), *O. obumbratus* Johannsen (16), and *O. oliveri* Soponis (17). While the 3 small species and 4 large species may be separated based solely upon size (Fig. 2), values for large and medium-sized species widely overlap due in part to the larger variances associated with increased size. The 3 small species, particularly *O. annectens* (1), appear to be distinctly smaller than many medium-sized species; however, as additional specimens of both small and medium-sized species become available these gaps will likely close.

PC2, which accounts for 10.22 to 15.21 percent of the variation (Tables 1-2), contrasts the number of radial setae with all remaining characters. Correlation coefficients between PC2 and characters other than R are small (Table 1) so that PC2 may be loosely referred to as the radial setae component. Species with large numbers of radial setae, such as *O. tryoni* Soponis (21, Fig. 3), will have large PC2 component scores, while species with small numbers of radial setae for their size, such as *O. annectens* (1), *O. hazenensis* Soponis (9), *O. nigritus* (15), and *O. subletti* Soponis (19), will have small component scores (Fig. 3). However, size plays a significant role in determining PC2 scores. In species with relatively constant radial setae counts, or small variances for R, such as *O. clarkei* Soponis (5), *O. obumbratus* (16), and *O. subletti* (19), large specimens will display slightly decreased PC2 scores due to the subtraction of increased values for the remaining characters, even though these characters are represented by very small coefficients (Table 1, Fig. 3).

PC2 separates *O. tryoni* (21) from several species with small component scores (Fig. 3) and suggests that *O. tryoni* could be separated from *O. annectens* (1), *O. hazenensis* (9), *O. nigritus* (15), and *O. subletti* (19) by R counts or a reduced PC2 variable such as 9(R) — ARM — WW, where the distance from the arculus to crossvein rm (ARM) and wing width (WW) are expressed in micrometers. The reduced PC2 variable correctly assigns all

specimens to species for the *O. tryoni* versus *O. nigritus* (n = 29) and *O. tryoni* versus *O. hazenensis* (n = 30) comparisons, while correctly separating 87.5 percent of the *O. tryoni* and *O. subletti* specimens (n = 24). However, the reduced PC2 variable could correctly separate only 45 percent of the specimens (n = 49) for the *O. tryoni* versus the small species *O. annectens* comparison. The reduced PC2 variable performs better than any single character such as R counts for large and medium-sized species, but not for comparisons between *O. tryoni* and smaller species such as *O. annectens*. Ninety-two percent of the specimens (n = 49) for an *O. tryoni* versus *O. annectens* comparison may be correctly separated based only upon R counts. Poor separation between *O. tryoni* and smaller species results from the subtraction of greater ARM and WW values in *O. tryoni,* which nullifies the differences in R counts between *O. tryoni* and smaller species. Despite size dependency, reduced PC2 variables may be potentially useful tools for separating particular species, and the use of radial setae counts merits further study.

PC3 accounts for 3.3 to 5.1 percent of the variation in the data, and contrasts the wing size and wing vein length characters, WL, WW, ARM, and AFCU (Fig. 1) with the number of squamal setae (Tables 1-2). Species with large component scores for PC3, such as *O. clarkei* (5, Fig. 4) have relatively small wings and large numbers of squamal setae, while species with small values for PC3, such as *O. decoratus* (Holmgren), (6, Fig. 4), have relatively large wings and small numbers of squamal setae. Size plays an important role in determining PC3 scores via the 4 wing characters. In species that do not display strong positive allometry for SQUM, such as *O. annectens* (1), *O. carlatus* (3), *O. clarkei* (5), *O. decoratus* (6), *O. dorenus* (8), *O. hazenensis* (9), *O. obumbratus* (16), and *O. oliveri* (17), larger specimens will have slightly smaller PC3 scores (Fig. 4).

Differences in PC3 scores (Fig. 4) between *O. clarkei* (5) and *O. decoratus* (6) suggest employment of a reduced PC3 variable to separate these species. The variable SQUM — WL can correctly separate 10 of 11 specimens for which data are available; however, a critical evaluation of this variable's ability to separate these species must await collection of additional specimens.

Literature Cited

Anderson, T.W. 1963. Asymptotic theory for principal component analysis. Ann. Math. Stat. 34:122-148.

Brundin, L. 1956. Zur Systematik der Orthocladiinae (Dipt. Chironomidae). Rep. Inst. Freshwat. Res. Drottningholm 37:5-185.

Humphries, J.M., F.L. Bookstein, B. Chernoff, G.R. Smith, R.L. Elder, and S.G. Poss. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30:291-308.

Jolicoeur, P. 1963a. The multivariate generalization of the allometry equation. Biometrics 19:497-499.

_____. 1963b. The degree of generality of robustness in *Martes americana*. Growth 27:1-27.

Mosimann, J.E. 1970. Size allometry: size and shape variables with characterization of the lognormal and generalized gamma distributions. J. Amer. Stat. Assoc. 65:930-945.

Oliver, D.R. 1977. *Bicinctus*-Group of the genus *Cricotopus* Van der Wulp (Diptera: Chironomidae) in the Nearctic with a description of a new species. J. Fish. Res. Bd. Can. 34:98-104.

Pimentel, R.A. 1979. Morphometrics the multivariate analysis of biological data. Kendall/Hunt, Dubuque. 276 pp.

Saether, O.A. 1976. Revision of *Hydrobaenus, Trissocladius, Zalutschia, Paratrissocladius* and some related genera (Diptera: Chironomidae). Bull. Fish. Res. Bd. Can. 195:1-287.

_____. 1977. Taxonomic studies on Chironomidae: *Nanocladius, Pseudochironomus,* and the *Harnischia* complex. Bull. Fish. Res. Bd. Can. 196:1-143.

Soponis, A.R. 1977. A revision of the Nearctic species of *Orthocladius (Orthocladius)* van der Wulp (Diptera: Chironomidae). Mem. Entomol. Soc. Can. 102:1-187.

Sprent, P. 1972. The mathematics of size and shape. Biometrics 28:23-27.

Townes, H.K., Jr. 1945. The Nearctic species of Tendipendini (Diptera, Tendipedidae (= Chironomidae)). Amer. Midl. Natur. 34:1-206.

Emergence of Polypedilum (Chironomidae) in a
Sand-Bottomed Stream of Northern Florida

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ABSTRACT. — Emergence data are given for 5 species of *Polypedilum: aviceps* Townes, *convictum* (Walker), *fallax* (Johannsen), *illinoense* (Malloch), and *scalaenum* (Schrank). Overlapping emergence occurs among all the species in Turkey Creek. During the summer *P. aviceps* may emerge downstream in Rocky Comfort Creek, a 4th order stream. Turkey Creek is probably a more favorable habitat for *P. aviceps* than for *P. convictum,* based on numbers and patterns of emergence. All species have longer emergence periods in Turkey Creek, Florida, than in L'Achigan River, Quebec, which is expected if latitude restricts seasonal emergence.

INTRODUCTION

Only a few North American studies have dealt with seasonal emergence of chironomids in lotic habitats at the species level, and all of these (Coffman 1973, Cloutier and Harper 1978, Harper and Cloutier 1979, Boerger 1981) have been conducted in streams and rivers above 40°N latitude. This paper is concerned with the seasonal emergence of 5 species of *Polypedilum* in Turkey Creek, Florida (30° N latitude). The emergence patterns and emergence periods of these species are compared with those of a higher latitude in North America. Corbet's (1964) theory of latitude restriction of seasonal emergence in North America holds for all 5 species: all species have longer emergence periods in Florida. Similarities and differences in emergence patterns are probably due to factors other than latitude, such as favorable or unfavorable habitat.

STUDY SITE AND METHODS

Turkey Creek is a 3rd order (Leopold et al. 1964), sand-bottomed stream located in Gadsden County, Florida (30° 29′ N, 84° 35′ W). At the sampling site the average depth was 15-30 cm, the average width, 4 m.

Pupal exuviae were collected in 2 drift nets, one placed 2 m and the other 1 m from the stream bank. These nets (735μm opening) were placed in the stream for 24 hrs biweekly from February 1979 to January 1980. Data from

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both nets were pooled. Species identifications were based on pupal associations of reared material, using the keys of Maschwitz (1976) for the larva, pupa, and adult.

The study site and methods are described in more detail in Soponis (1980). This study is based on 280 specimens.

RESULTS AND DISCUSSION

Emergence data for the 5 species of *Polypedilum* are presented in Fig. 1. *P. aviceps* and *P. fallax* emerge during the winter months with no emergence from May to September/October. *P. illinoense* emerges during a similar period, and, in addition, a single exuvium was collected in August. *P. convictum* emerges throughout the year except for the winter months of December, January, and February. *P. scalaenum* emerges in 3 waves throughout the year.

Harper and Cloutier (1979) reported on the emergence for the same 5 species in the higher latitude stream, L'Achigan River, Quebec (46°N, 74°W). The emergence of these species is longer in Turkey creek (6 to 9 months) than in L'Achigan River (3 to 4 months). *P. convictum* emerges from mid-May to mid-August in Quebec, and March to November in Florida. *P. scalaenum* emerges in June in Quebec, but in June and 7 other months in Florida. *P. aviceps* and *P. fallax* emerge May to September in Quebec, and October/November to May in Florida. *P. illinoense* emerges from June to August in Quebec, and from November to June, and August in Florida. Shorter periods of emergence of aquatic insects are typical of higher latitudes in North America, probably as a result of temperature (Corbet 1964).

Patterns of emergence are strikingly different for *P. convictum* in the 2 streams. In Turkey Creek *P. convictum* has an amodal emergence whereas in L'Achigan River it has bimodal to trimodal emergence. The differences in patterns may be due to the numbers of specimens collected which, aside from collecting techniques, may reflect favorable or unfavorable conditions for the species. The low numbers (n = 16) and amodal emergence suggest that Turkey Creek is not a favorable habitat for *P. convictum,* and that L'Achigan River is. By contrast, the large numbers (n = 186) and distinct pattern of *P. aviceps* suggest that Turkey Creek and L'Achigan River are favorable habitats for this species. However, this needs to be confirmed with more study. I agree with Harper and Cloutier (1979) that variations in emergence patterns of the same species in different sites and in different years reflect the favorableness of the habitat for the species at that place and time.
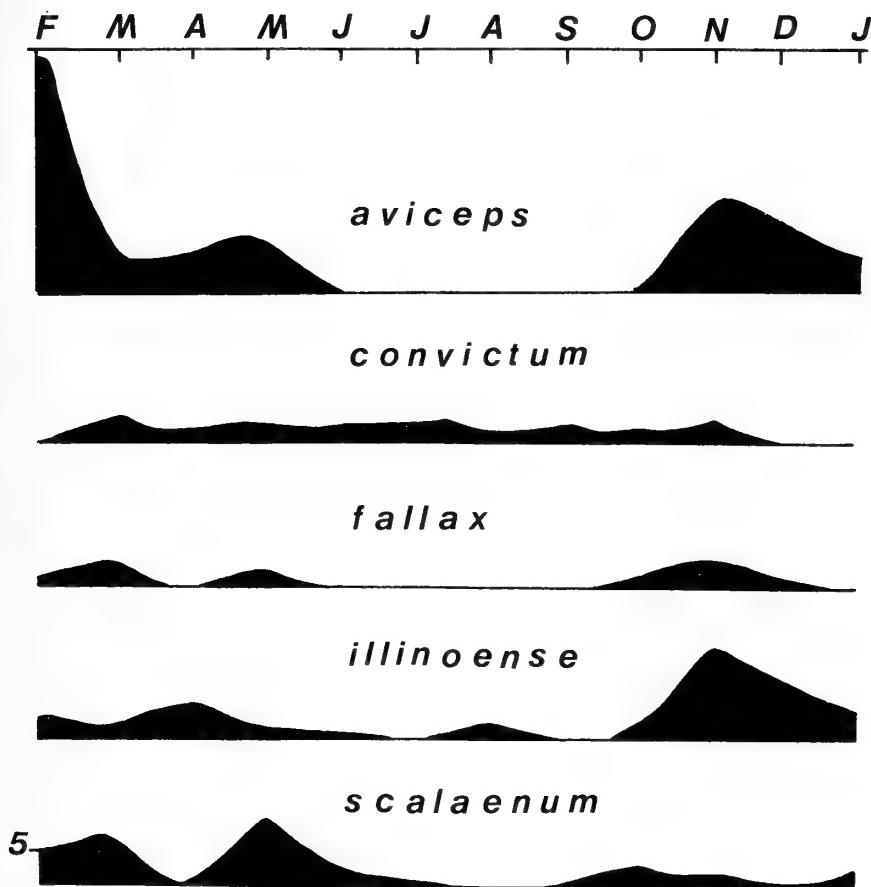
FIG. 1. Emergence of 5 species of *Polypedilum* from February 1979 to January 1980. Numbers of pupal exuviae on vertical axis, months on horizontal axis.

P. aviceps emerges in Turkey Creek in months (November to May) that are almost complementary to those (May to September) in L'Achigan River. This might suggest that *P. aviceps,* a lotic species often found in northern waters (Maschwitz 1976, Harper and Cloutier 1979, Boerger 1981) is cold-adapted and has switched its life cycle in Florida to take advantage of the cooler months. However, life history data on *Polypedilum* in Turkey Creek (Russell and Soponis, unpub.) suggest that *P. aviceps* is also emerging in the summer because large numbers of 3rd and 4th larval instars are drifting in late May and June. If this is true and adults are emerging, but

pupal skins are not recovered in Turkey Creek, then it raises the possibility that *P. aviceps* is emerging downstream.

There is some indirect evidence to support downstream emergence of *P. aviceps*. Iovino and Miner (1970) collected adults of *P. aviceps* in emergence traps in an Arkansas reservoir in June, July, and September. However, they were unable to find the larvae in spite of sampling the benthos for one year. In the same study they found low level, transient populations of certain species in the reservoir, mostly orthoclads, which they attributed to an influx from spring-fed streams. The possibility exists that larvae of *P. aviceps* drifted from the streams into the reservoir and emerged there.

It seems likely that *P. aviceps* from Turkey Creek could emerge in the summer in Rocky Comfort Creek. In Turkey Creek, larvae of *P. aviceps* inhabit leaf packs in the current. Turkey Creek joins a 4th order stream, Rocky Comfort Creek, 0.36 km downstream. Rocky Comfort Creek empties into Lake Talquin, which in 5.7 km downstream from the collecting site on Turkey Creek. It's unlikely that such lotic larvae would survive in the lentic conditions of Lake Talquin. Dendy (1944) showed that many stream dwelling chironomid larvae that drifted into lakes died there. Although Ward and Cummins (1978) found larvae of *Paratendipes albimanus* (Mg.) in a lake as well as 1st to 3rd order streams, *P. albimanus* is primarily a lentic species. Further study is needed to confirm the downstream emergence of *P. aviceps*.

Overlapping emergence occurs in all 5 species in Turkey Creek. In all months except September at least 2 species are emerging at the same time. In March and May all congeners are on the wing. This seems to be true of *Polypedilum* in 2 other streams. In Linesville Creek, Pennsylvania, Coffman (1973) recorded the emergence of 5 species of *Polypedilum* in June, and 4 of these were on the wing from June to August. In L'Achigan River, 16 species of *Polypedilum* emerged from May to September. However, in Bigoray River, Alberta, Boerger (1981) found no overlap between *Polypedilum scalaenum* and *Polypedilum braseniae* (Leathers). Boerger did not report the emergence for 4 less common species of *Polypedilum,* and I suspect that emergence of some of the species overlap.

Since lotic habitats support many species of *Polypedilum,* complex resource partitioning by the larvae can be expected. Harper and Cloutier (1979) found evidence that *P. aviceps* dominates the lower part of riffles, and *P. convictum* dominates the upper part. In Turkey Creek, at least 3 species of *Polypedilum* partition the leaf pack habitat (Russell and Soponis, unpub.).

In summary, species of *Polypedilum* are found emerging from many lotic habitats in North America, and the same species are found in streams of different latitudes. Species do tend to have longer emergence periods at lower

latitudes as Corbet predicts. Overlapping emergence appears to be common within the genus although some species do not overlap in the same habitat. Differences in species patterns of emergence may indicate the favorableness of the species habitat.

LITERATURE CITED

BOERGER, H. 1981. Species composition, abundance and emergence phenology of midges (Deiptera: Chironomidae) in a brown-water stream of West-Central Alberta, Canada. Hydrobiol. 80: 7-30.

CLOUTIER, L. AND P.P. HARPER. 1978. Phénologie de Tanypodinae de ruisseaux des Laurentides (Diptera; Chironomidae). Can. J. Zool. 56:1129-1139.

COFFMAN, W.P. 1973. Energy flow in a woodland stream ecosystem: II. The taxonomic composition and phenology of the Chironomidae as determined by the collection of pupal exuviae. Arch. Hydrobiol. 71:281-322.

CORBET, P.S. 1964. Temporal patterns of emergence in aquatic insects. Can. Entomol. 96:264-279.

DENDY, J.S. 1944. The fate of animals in stream drift when carried into lakes. Ecol. Mongr. 14:333-357.

HARPER, P.P. AND L. CLOUTIER. 1979. Chironomini and Pseudochironomini of a Québec highland stream (Diptera: Chironomidae). Entomol. Scand. Suppl. 10:81-94.

IOVINO, A.J. AND F.D. MINER. 1970. Seasonal abundance and emergence of Chironomidae of Beaver Reservoir, Arkansas (Insecta: Diptera). J. Kansas Entomol. Soc. 43:197-216.

LEOPOLD L.B., M.G. WOLMAN, AND J.P. MILLER. 1964. Fluvial processes in geomorphology. W.H. Freeman and Co.: San Francisco, 522 pp.

MASCHWITZ, D.E. 1976. Revision of the nearctic species of the subgenus *Polypedilum* (Chironomidae: Diptera). Ph.D. thesis, Univ. of Minnesota, 325 pp.

SOPONIS, A.R. 1980. Taxonomic composition of Chironomidae (Diptera) in a sand-bottomed stream of northern Florida, pp. 163-169. IN: Murray, D.A. (Ed.), Chironomidae Ecology, Systematics, Cytology, and Physiology. Pergamon Press: New York.

WARD, G.M. AND K.W. CUMMINS. 1978. Life history and growth patterns of *Paratendipes albimanus* in a Michigan headwater stream. Ann. Amer. Entomol. Soc. 71:272-284.

Communities of Chironomidae (Diptera) from an acid-stressed headwater stream in the Adirondack Mountains, New York

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Abstract. — During the summer of 1980 the benthic invertebrates of Silver Run, a small headwater stream in the Adirondack Mountains of upstate New York, and its tributaries were investigated to document differences between tributaries with different pH. Communities of Chironomidae in strongly acidic first-order streams (pH 4.48-5.20) contained 40-70% fewer taxa than the community in a physically comparable, less acidic stream (pH 5.72-6.71). The acidobiontic (strongly acidic) communities were strongly dominated by one or more of the following taxa: *Conchapelopia americana/flavifrons*, *Eukiefferiella claripennis* gr., *Cricotopus tremulus* gr., and *Cricotopus vierriensis*.

These results suggest that communities of Chironomidae respond to decreased pH in much the same way as do total macroinvertebrate communities: many species are replaced with a few dominant ones.

Introduction

The acidification of precipitation and surface waters in eastern North America is well documented (see summary by Haines 1981; also Cogbill 1976, Cogbill and Likens 1974, Likens and Bormann 1974, Likens *et al.* 1979). Surface waters at high altitudes, such as the Adirondack and White Mountain regions, are particularly susceptible to acidification. Because their geologic substrates are highly resistant to chemical weathering, there is little buffering of the acid before precipitation enters the surface water systems (Hall *et al.* 1980).

The present study was part of a project to document differences in the biota of a small stream in the Adirondack Mountains whose tributaries exhibit varying degrees of acidity. Information concerning the midge fauna will be presented here. Data concerning the total macroinvertebrate fauna will be presented elsewhere (Simpson and Bode, in preparation).

Study Area

Silver Run is a small, short headwater stream located approximately 20 km south-southwest of the village of Blue Mountain in Hamilton County,

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New York (latitude 43°42′, longitude 74°35′) (Fig. 1). It originates at about 850 m elevation, flows west and then southwest, and discharges to the South Branch of the Moose River, which eventually flows via the Black River into Lake Ontario.

Silver Run falls 150 m over its course of 6.2 km and receives two main tributaries, Cellar Brook and Bradley Brook, 2.4 and 1.3 km from its mouth, respectively.

This system is attractive for study because of the different pH in the physically similar streams. Between April and September 1980, Silver Run upstream of Cellar Brook ranged from pH 5.72 to 6.71. Based on definitions established by the US Environmental Protection Agency (Harris and Lawrence 1978, Hubbard and Peters 1978, Surdick and Gaufin 1978), the fauna at this site is acidophilic (occurring at pH 5.5-7.0). During the same period, Cellar Brook and Bradley Brook ranged from pH 4.48 to 5.20; their faunas are classified as acidobiontic (occurring at pH less than 5.5).

The different pH regimes in these streams may be related to stream gradient. Cellar and Bradley brooks flow through high-gradient mountain valleys with little accumulated soil to buffer the water. Silver Run originates in a lower-gradient area.

As would be expected, pH values in Silver Run downstream of the tributaries reflected the combined flow of the three source waters, ranging from 4.82 to 6.22.

Samples were collected at four sites: (1) Silver Run upstream of both tributaries, (2) Cellar Brook near its mouth, (3) Bradley Brook near its mouth, and (4) Silver Run downstream of both tributaries (Fig. 1). Stations 1-3 were all on first-order streams and were very similar with regard to flow (Table 1), width (5-6 m), and current speed (10-20 cm/sec). Although station 4 was considerably wider (18 m) and had higher flows, samples could be collected from areas with similar depth and current speed.

The substrate at stations 1 and 2 consisted of rubble 3-20 cm in diameter with sand and gravel underneath. The substrate at stations 3 and 4 was similar but also contained numerous larger rocks, some several meters in diameter.

Methods

Macroinvertebrates were sampled quantitatively with a Surber square-foot sampler (net mesh size = 1.05 mm). All rocks within the square frame were removed and thoroughly cleaned, and the underlying sand and gravel were agitated to a depth of about 10 cm. Three samples were taken at each site on 2 July 1980 and three on 9 September 1980. The samples were
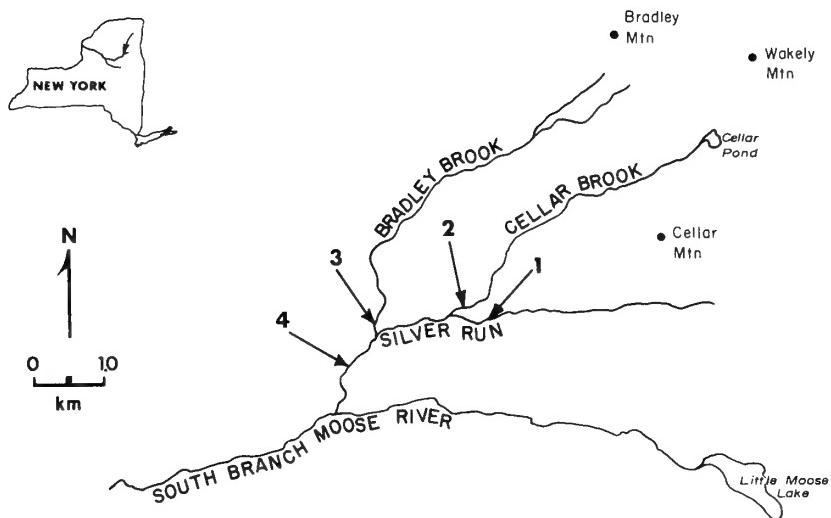
Fig. 1.   Map of Silver Run and tributaries, showing locations of sampling sites.

preserved in 70% ethanol with rose bengal stain (Mason and Yevich 1967) and later picked under a dissecting microscope. Midges were cleared in warm KOH (10%), rinsed successively in water and ethanol, and mounted in Euparal.

Communities of midges were characterized by taxonomic richness and the number of individuals per sample. Diversity indices were not used due to the small sample size (Weber 1973). Even when all three samples were pooled, fewer than 100 individuals were obtained at any site. Pooled samples were used to assess changes in taxonomic richness; however, means of the values for individual samples showed the same trends.

To evaluate trends in the occurrence of individual taxa, only those occurring in two or more samples at any one site were used. These are termed common taxa.

RESULTS

The taxa found at each sampling site are listed in Table 2.

At station 1, the Orthocladiinae were dominant in terms of both the number of taxa and the number of individuals contributed to the total midge fauna (Fig. 2). The Tanytarsini were the second most abundant, followed by the Tanypodinae and Chironomini.

TABLE 1. Some physico-chemical parameters of Silver Run and tributaries (based on 9 measurements taken between 3 April and 29 September 1980).

Station/Location	pH			Temperature (°C)			Flow (m³/s)			Conductivity (μS)		
	Median	Min	Max	Median	Min	Max	Median	Min	Max	Median	Min	Max
1—Upper Silver Run	6.15	5.68	6.71	8	2	15	0.17	0.06	0.51	30	27	32
2—Cellar Brook	4.60	4.50	5.20	9	3	18	0.30	0.06	0.68	35	27	42
3—Bradley Brook	4.65	4.48	4.95	9	2	17	0.20	0.08	0.74	38	32	45
4—Lower Silver Run	5.15	4.82	6.22	11	6	18	0.89	0.23	1.90	32	27	35

The midge fauna at station 1 was not strongly dominated by any particular taxon. The two most abundant taxa collectively comprised 27% of the total individuals in July and 40% in September. Numerous rare organisms were also found at this site: 11 taxa were represented by only one individual in the six pooled Surber samples (July plus September).

Eleven taxa occurred in two or more samples at station 1 (Table 3) and appeared to be important components of the community. In July, three of these common taxa were Tanytarsini, two were Orthocladiinae, and one was Tanypodinae. In September all six common taxa were Orthocladiinae. Only *Rheocricotopus* sp. was commonly found during both sampling periods.

At stations 2 and 3, the structure of the midge community was markedly different than at station 1. Many fewer taxa (40-70%) were collected at each site, and the two most abundant taxa contributed a much greater proportion to the total number of individuals (as much as 90%). Although the number of orthoclad taxa was 50% lower, this group still contributed the most taxa and individuals to the total community. The contribution of Tanytarsini declined from 30% of the total individuals at station 1 to an average of 3% at stations 2 and 3.

Only five taxa were common in the acidobiontic communities at stations 2 and 3 (Table 4): one Tanypodinae and four Orthocladiinae. *Conchapelopia americana/flavifrons*[1] was common at one or both sites during both months and was dominant at station 3 in September. *Eukiefferiella claripennis* group was common at both sites in July and comprised 75% of the individuals at station 3. *Cricotopus tremulus* group and *Cricotopus vierriensis* Goetgh. occurred during both months but were common and more abundant in September.

Station 4 yielded the same number of taxa as station 3 but substantially fewer individuals than any of the other sampling sites. An average of only 7 individuals per Surber sample was obtained (= 75 individuals/m² of streambed). *Eukiefferiella claripennis* group was the only common taxon, and it was common during both sampling periods. No Tanytarsini were collected at this site.

A comparison of the fauna found at station 1 versus those found at stations 2-4 demonstrates the paucity of taxa in the more strongly acidified

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[1]*Conchapelopia americana* Fittkau and *C. flavifrons* (Joh.) occurred concurrently in our samples. Species identifications were made on mature (4th instar) larvae using Roback's (1981) key characters of size and were verified with pupal characters visible in prepupal specimens. Most samples contained numerous early instars that could not be identified with certainty, hence the designation *Conchapelopia americana/flavifrons*.

TABLE 2. Pooled abundances of Chironomidae in three Surber samples; Silver Run and tributaries (* = occurred in 2 samples; ** = occurred in 3 samples; all others occurred in 1 sample).

Date (1980)	2 July				9 September			
Station	1	2	3	4	1	2	3	4
Tanypodinae								
Ablabesmyia mallochi (Walley)	5	•	•	•	•	•	•	•
Conchapelopia americana Fittkau/ flavifrons (Joh.)	6**	9*	8**	•	•	2	38**	3
Nilotanypus fimbriatus (Walker)	1	•	•	•	•	•	•	•
Zavrelimyia sp.	•	2	1	•	•	1	•	•
Orthocladiinae								
Cricotopus bicinctus (Meigen)	1	•	•	•	6	•	•	•
Cricotopus nr. flavocinctus	1	5	•	1	3	•	•	•
Cricotopus tremulus gr.	1	2	3	4	•	10*	15*	•
Cricotopus vierriensis Goetgh.	•	6	•	1	13*	14**	1	1
Cricotopus (Isocladius) sp.	1	•	•	•	•	•	•	•
#Cricotopus/Orthocladius sp.	•	•	•	•	6*	•	•	•
Eukiefferiella brehmi gr.	3	3	•	•	•	•	•	•
Eukiefferiella claripennis gr.	•	8**	41**	13**	5	•	2	5
Eukiefferiella devonica gr.	•	•	•	•	1	•	•	•
Heterotrissocladius hirtapex? Saether	•	•	•	•	•	1	3*	•
Krenosmitta sp.	1	•	•	•	•	•	•	•
Mesocricotopus sp.	8**	•	•	•	•	•	•	•
Parakiefferiella sp. 2	1	•	•	•	•	•	•	•
Parametriocnemus lundbecki (Joh.)	•	•	•	•	7*	•	•	•
Rheocricotopus sp.	2*	•	•	2	7**	•	•	•
Synorthocladius nr. semivirens	5	1	•	•	3	•	•	•
Thienemanniella nr. xena	•	1	1	•	5**	2	•	•
Tvetenia bavarica gr.	1	•	•	•	3*	•	•	•

	1	2	3	4	5	6	7	8
Chironominae								
Chironomini								
Dicrotendipes neomodestus (Malloch)	•	•	•	•	1	•	•	•
Glyptotendipes sp.	1	•	•	•	•	2	•	8
Polypedilum aviceps Townes	1	•	•	2	•	•	•	•
Polypedilum convictum (Walker)	1	•	•	•	•	•	•	•
Polypedilum illinoense (Malloch)	1	1	•	•	•	•	•	•
Tanytarsini								
Micropsectra polita? (Malloch)	2*	1	•	•	•	•	•	•
Rheotanytarsus exiguus gr.	6*	•	•	•	•	•	•	•
Stempellinella sp.	2	•	•	•	•	•	•	•
Tanytarsus brundini Lind.	8**	•	1	•	3	•	•	•
Tanytarsus guerlus gr.	1	•	•	•	•	•	•	•
#Undetermined	•	•	•	•	20	4	•	1
Number of individuals	59	38	55	23	83	36	59	18
Number of taxa	22	10	6	6	14	8	5	5

#early instars

streams. The six Surber samples from station 1 yielded 30 midge taxa, including all those listed in Table 2 except *Zavrelimyia* sp., *Heterotrissocladius hirtapex?* Saether, and *Glyptotendipes* sp. In contrast, the 18 samples from stations 2-4 collectively contained only 16 taxa. If mere presence is used to determine a taxon's environmental requirements, these 16 taxa could be classified as acidobiontic.

DISCUSSION

The number of midge taxa (33) found during the course of this study is relatively low, considering that intensive studies of other small streams have yielded over 100 species (Coffman 1973, Ringe 1974, Boerger 1981). A complete species list for the system would doubtless be considerably longer, especially if drift and emergence samplers were utilized. The number of individuals collected is also very meager, considering that midge densities in small streams (first- to third-order) often range from several hundred to several thousand individuals per m² (e.g., Newbold *et al.* 1980, Pinder 1980). These sparce results may reflect ineffective sampling to some degree, but they are also due in part to the oligotrophic nature of high-altitude mountain streams (Pennak 1977).

Members of the subfamily Orthocladiinae are well known for dominating the midge fauna in small streams (Brennan *et al.* 1981, Coffman 1973, Drake 1982, Pinder 1980, Thienemann 1954). Thus, their predominance in the Silver Run system is not surprising. However, the absence of Diamesinae was unexpected. The physical traits of the stream seem well suited for them, and some species are reported to be acid-tolerant (Curry 1965, Scullion and Edwards 1980). Some resident species may have been missed because there was no winter sampling, when many diamesin species are most active.

Midges are important in the macroinvertebrate communities of acidified streams, although they often are identified only to the family level (Arnold *et al.* 1981, Sutcliffe and Carrick 1973, Pratt and Hall 1981). More precise taxonomic work could enhance the results of such studies. For example, reduced species richness has been cited repeatedly as a major biological effect of increased acidity (Haines 1981, Hall *et al.* 1980). Since midge richness also declines substantially, accurate identification of midges would amplify the observed reduction in taxonomic richness of the total macroinvertebrate community.

One approach toward understanding the effects of acidification is to compile a list of acidobiontic taxa. The occurrence of relatively few taxa in severely stressed waters facilitates the development of a species assemblage
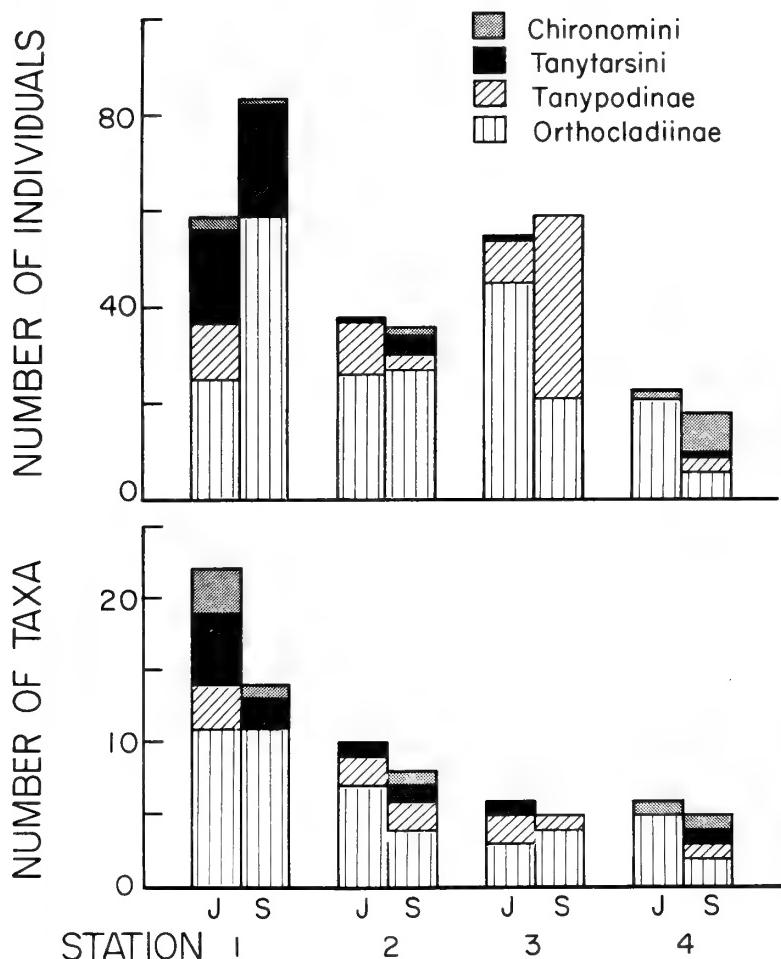
FIG. 2.   Number of individuals and number of taxa of midges collected in Silver Run and tributaries, July (J) and September (S), 1980. Results are composites of 3 Surber samples for each collection site and time.

indicative of such conditions. *Conchapelopia* contains some of the most successful inhabitants of strongly acidified streams. In addition to our observations regarding *Conchapelopia americana* and *C. flavifrons*, Roback (1981) reported these same species as occurring in water with pH 4.1 to 7.0. Along with "*C. flavifrons* var." these are the only members of the *Thienemannimyia* group found at pH 4.1 to 5.0. Scullion and Edwards

TABLE 3.   Common acidophilic Chironomidae in the Silver Run system (those occurring in 2 or more samples from station 1).

Taxon	July	September
Conchapelopia americana/flavifrons	X	
Cricotopus vierriensis		X
Cricotopus/Orthocladius sp.		X
Mesocricotopus sp.	X	
Parametriocnemus lundbecki		X
Rheocricotopus sp.	X	X
Thienemanniella nr. *xena*		X
Tvetenia bavarica gr.		X
Micropsectra polita?	X	
Rheotanytarsus exiguus gr.	X	
Tanytarsus brundini?	X	

TABLE 4.   Common acidobiontic Chironomidae in the Silver Run system (those occurring in 2 or more samples from Cellar Brook and/or Bradley Brook).

Taxon	July	September
Conchapelopia americana/flavifrons	X	X
Cricotopus tremulus gr.		X
Cricotopus vierriensis		X
Eukiefferiella claripennis gr.	X	X
Heterotrissocladius hirtapex?		X

(1980) reported *Conchapelopia pallidula* (Mg.) as one of only two insects found in a small stream with pH less than 3.5.

Eukiefferiella claripennis group is the most tolerant group in the genus *Eukiefferiella* to a number of environmental perturbations, including low pH (Bode, 1983). Larvae of *E. claripennis* (Lundb.) have been found in alkaline chalk streams with pH above 8.0 (Pinder, personal communication). Roback (1974) reported "*Eukiefferiella* sp." as occurring at pH greater than 8.5. Further taxonomic work must be done to determine if species in this group have different pH tolerances or if a single species can tolerate a wide range of pH.

Although *Cricotopus* is one of the most common and widely distributed lotic midge genera, I could find little information regarding its occurrence in acidified waters. Data presented by Beck (1977), Curry (1965) and Roback (1974) suggest that most species prefer neutral or slightly alkaline waters.

Many midges are adversely affected by decreased pH. For example, Pratt and Hall (1981) tentatively recommended midges (and mayflies) as in-

dicators of acid precipitation in small mountain streams, based on increased drift rates in response to experimental acidification. Their study documented the sensitivity of midges as a group to decreased pH, but it did not distinguish between sensitive and tolerant taxa because the midges were identified only to the subfamily level.

Except for *Conchapelopia americana/flavifrons* and *Cricotopus vierriensis,* all of the common acidophilic taxa in our study (Table 3) were much less abundant or absent in the acidobiontic communities. Although some of these taxa probably are limited directly or indirectly by low pH, considerable additional sampling would be necessary to confirm that the observed distributions were not due to sampling variability. Moreover the responses of the same species may be different in other streams due to differences in stream chemistry. Haines (1981) discussed discrepancies between reported responses of congeneric organisms to decreased pH and warned of the difficulty of determining cause and effect relationships in complex ecosystems. Some of the taxa which appear acid-sensitive in the present study are in genera reported by Scullion and Edwards (1980) to contain acid-tolerant representatives (*Micropsectra, Rheocricotopus, Rheotanytarsus, Tanytarsus*). Additional work must be done to produce a list of acid-sensitive midge species.

It is beyond the scope of this work to discuss in detail the many ways in which low pH can affect biological communities. Haines (1981) and Sutcliffe and Carrick (1973) discuss several potential mechanisms. In high-elevation areas of the Northeast mobilization of aluminum at low pH is thought to be a particularly important consequence of acid precipitation, with severe biological and ecological ramifications (Cronan and Schofield 1979, Hall *et al.* 1980). In Silver Run, low pH is evidently not solely responsible for the observed differences in the midge fauna. If it were, station 4 should support a fauna intermediate between that found at station 1 and those found at stations 2 and 3.

Department of Environmental Conservation. Drs. Peter Cranston and Clive Pinder determined the proper placement of *Tanytarsus brundini?* (= *Micropsectra curvicornis* sensu Chernovskii). Mr. Bode and Drs. C.O. Berg and G.W. Fuhs critically reviewed the manuscript.

LITERATURE CITED

ARNOLD, D.E., P.M. BENDER, A.B. HALE AND R.W. LIGHT. 1981. Studies on infertile, acidic Pennsylvania streams and their benthic communities. pp. 15-33. *In* R.L. Singer, (ed.), Effects of acid precipitation on benthos. North Amer. Benthol. Soc. ISBN 0-941908-00-3. 154 pp.

BECK, W.M., JR. 1977. Environmental requirements and pollution tolerance of common freshwater Chironomidae. EPA-600/4-77-024. 261 pp.

BODE, R.W. 1983. Larvae of the North American *Eukiefferiella* and *Tvetenia* (Diptera: Chironomidae). N.Y.S. Museum Bull. No. 452. 40 pp.

BOERGER, H. 1981. Species composition, abundance and emergence phenology of midges (Diptera: Chironomidae) in a brownwater stream of West-Central Alberta, Canada. Hydrobiol. 80:7-30.

BRENNAN, A., A.T. WALENTOWICZ AND A.J. McLACHLAN. 1981. Midges (Diptera: Chironomidae) from the upper reaches of a spate river. Hydrobiol. 78:147-151.

COFFMAN, W.P. 1973. Energy flow in a woodland stream ecosystem: II. The taxonomic composition and phenology of the Chironomidae as determined by the collection of pupal exuviae. Arch. Hydrobiol. 71(3):281-322.

COGBILL, C. 1976. The history and character of acid precipitation in eastern North America. U.S. Forest Serv. Gen. Tech. Rep. NE-23:363-370.

COGBILL, C. AND G. LIKENS. 1974. Acid precipitation in the northeastern United States. Water Resources Res. 10:1133-1137.

CRONAN, C.S. AND C.L. SCHOFIELD. 1979. Aluminum leaching to acid precipitation: effects on high elevation watersheds in the Northeast. Science 204:304-306.

CURRY, L.L. 1965. Survey of environmental requirements for the midge (Diptera: Tendipedidae). pp. 127-141. *In* Biological problems in water pollution, 3rd seminar, 1962. U.S. Public Health Serv. Publ. No. 99-WP-25. 424 pp.

DRAKE, C.M. 1982. Seasonal dynamics of Chironomidae (Diptera) on the Bulrush *Schoenoplectus lacustris* in a chalk stream. Freshwater Biol. 12:225-240.

HAINES, T.A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110:669-707.

HALL, R.J., G.E. LIKENS, S.B. FIANCE AND G.R. HENDREY. 1980. Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 61(4):976-989.

HARRIS, T.L. AND T.M. LAWRENCE. 1978. Environmental requirements and pollution tolerance of Trichoptera. EPA-600/4-78-063. 310 pp.

HUBBARD, M.D. AND W.L. PETERS. 1978. Environmental requirements and pollution tolerance of Ephemeroptera. EPA-600/4-78-061. 461 pp.

LIKENS, G. AND F. BORMANN. 1974. Acid rain: a serious regional environmental problem. Science 184:1176-1179.

LIKENS, G., R. WRIGHT, J. GALLOWAY AND T. BUTLER. 1979. Acid rain. Sci. Amer. 241(4):43-51.

MASON, W.T. JR. AND P.P. YEVICH. 1967. The use of phloxine B and rose bengal stains to facilitate sorting benthic samples. Trans. Am. Microsc. Soc. 86(2):221-223.

NEWBOLD, J.D., D.C. ERMAN AND K.B. ROBY. 1980. Effects of logging on macroinverte-brates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37:1076-1085.

PENNAK, R.W. 1977. Trophic variables in Rocky Mountain trout streams. Arch. Hydrobiol. 80(3):253-285.

PINDER, L.C.V. 1980. Spatial distribution of Chironomidae in an English chalk stream. *In* D.A. Murray, (ed.), Chironomidae—ecology, systematics, cytology and physiology. Pergamon Press, New York, pp. 153-161.

PRATT, J.M. AND R.J. HALL. 1981. Acute effects of stream acidification on the diversity of macroinvertebrate drift. pp. 77-95. *In* R.L. Singer (ed.), Effects of acid precipitation on benthos. North Amer. Benthol. Soc. ISBN 0-941908-00-3. 154 pp.

RINGE, F. 1974. Chironomiden Emergenz 1970 in Breiten und Rohr wiesenbach. Arch. Hydrobiol. Suppl. 45:212-

ROBACK, S.S. 1974. Insects (Arthropoda: Insecta). Chapter 10. *In* C.W. Hart, Jr. and S.L.H. Fuller, (eds.), Pollution ecology of freshwater invertebrates. Academic Press, New York, 389 pp.

————. 1981. The immature chironomids of the eastern United States. V. Pentaneurini-*Thienemannimyia* group. Proc. Acad. Natur. Sci. Philadelphia 133:73-127.

SCULLION, J. AND R.W. EDWARDS. 1980. The effects of coal industry pollutants on the macroinvertebrate fauna of a small river in the South Wales coal field. Freshwater Biol. 10:141-162.

SIMPSON, K.W. AND R.W. BODE. In preparation. The macroinvertebrate fauna of Silver Run, a mountain stream system with variable acidity.

SURDICK, R.F. AND A.R. GAUFIN. 1978. Environmental requirements and pollution tolerance of Plecoptera. EPA-600/4-78-062. 417 pp.

SUTCLIFFE, D.W. AND T.R. CARRICK. 1973. Studies on mountain streams in the English Lake District. I. pH, calcium and the distribution of invertebrates in the River Duddon. Freshwater Biol. 3:437-462.

THIENEMANN, A. 1954. Chironomus. Leben, Verbreitung und wirtschaftliche Bedeutung der Chironomiden. Binnengewasser 20:1-834.

WEBER, C.I. (ED.). 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. EPA-670/4-73-001.

Paracricotopus mozleyi n. sp. from Georgia, U.S.A.
(Diptera: Chironomidae)

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ABSTRACT. — The adult male, pupa and larva of *Paracricotopus mozleyi* n. sp. were collected from a vertical rock seep in Lumpkin County, GA. All stages are described and illustrated and characters are given to distinguish the life stages of this species from the other species of the genus. This is the second species of *Paracricotopus* to be described from North America.

Saether (1980) described *Paracricotopus glaber* and revised the genus which contained two other species, the palearctic *P. niger* Kieffer and *P. uliginosis* Brundin. He placed *Paracricotopus* Thienemann and Harnisch into a group with *Nanocladius* Kieffer, *Mesocricotopus* Brundin, *Psectrocladius* Kieffer, and *Rheocricotopus* Thienemann and Harnisch. Saether's new species, *P. glaber* was described from three associated specimens collected from a seepage area on a mountainside outcrop in Oconee County, South Carolina. Recently, I collected specimens of a new, species, *P. mozleyi,* from a similar rocky seepage area in Lumpkin County, Georgia. The adult male, pupa and the larva of *P. mozleyi* are described here following the morphological terminology of Saether (1980a). The measurements are in microns and are expressed as means or ranges.

Paracricotopus mozleyi n. sp.

Type locality: Vertical rock seep 4.2 km northeast of Stonepile Gap crossroads on north side of State Route 60, Lumpkin County, Georgia. Elevation: 781 m.

Type Material: Holotype: pharate male and pupal skin (recovered from salamander gut). *Paratypes:* reared pharate male with cast pupal and larval skins, 1 pupal skin, 1 partial pupal skin, 2 4th instar larvae, 1 4th instar larval head (recovered from salamander gut), 1 3rd instar larva. All specimens collected by John W. Steiner, 26 X. 81. All in coll. U.S. Nat. Mus.

Diagnosis: The life stages of *P. mozleyi* n. sp. can be distinguished from

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those of *P. glaber* and *P. niger* by these combinations of characters: *Adult male:*   anal point proper without setae but with 3-4 setae at base; squama with 3-4 setae; inferior volsella apparently weak; last three palpal segments as 62:80:100. *Pupa:*   tergites VII-IX with anterior shagreen; largest precorneal seta longer than thoracic horn. *Larva:* last three antennal segments subequal; Lauterborn organs longer than segment III.
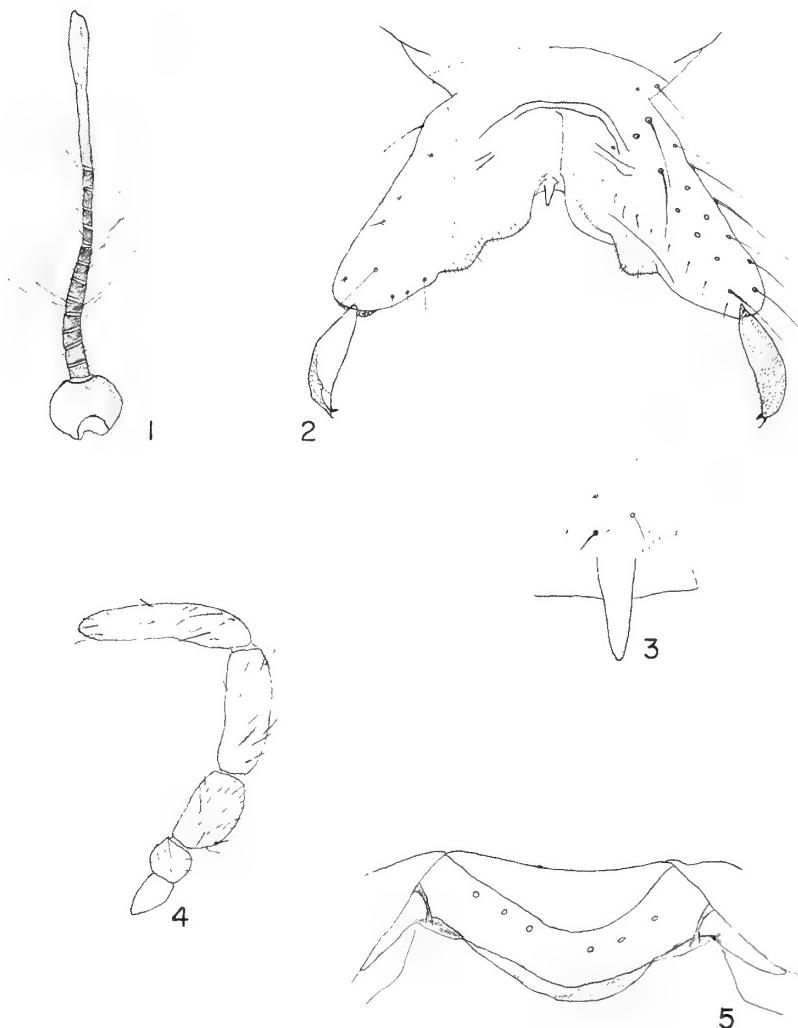
FIGS. 1-5.   *Paracricotopus mozleyi* n. sp. *Male* — 1. Antenna. — 2. Hypopygium (right, ventral view; left, dorsal view). — 3. Anal point. — 4. Palpus. — 5. Scutellum.

Etymology: This species is named in honor of Dr. Sam Mozley of North Carolina State University.

MALE (n = 2: both pharate)
Dark olive-brown body with red eyes. Total length about 3200.

Head: eyes hairy, diameter of largest facet 10. Palpal segments (Fig. 4) in the ratio: 27:25:60:80:100. Outer vertical setae 2. Antenna (Fig. 1.) with 13 flagellomeres in the ratio: 33:23:20:20:27:27:30:30:28:27:26:26:268; AR: 0:84.

Thorax: scutellum (Fig. 5) with six strong setae. Dorsocentral setae 6-9; prealars 3. Haltere dark.

Wing: Squama with 3-4 setae.

Hypopygium: anal point proper (Fig. 3) very small and without setae, length 8-11, base with 3-4 setae. Gonocoxite length 175, gonostylus (Fig. 2) length 83. Laterosternite IX with 2-3 setae. HR: 1.92-2.14.

PUPA (n = 4)
Light Brown with darker spines. Total length 3070.

Cephalothorax: length 1270. Thoracic horn (Fig. 7) entirely smooth or with two shallow lateral notches, length 95. Anterior precorneal seta length 125; median precorneal seta length 105. Median anteprontal setae 2, length of each about 90. Dorsum of cephalothorax weakly reticulate. Dorsocentral setae 4, distance between 1st and 2nd 50. Wing sheaths smooth.

Abdomen: length 1800. Anterior shagreen on tergites VII-IX (Fig. 8). Median or posterior shagreen on sternites II-VIII. Numbers of large (8 +) spines in median transverse rows on T III-VII as 8-20, 20-24, 20-29, 18-26, 0-3; numbers of small (8 −) spines in same rows as 6-10, 9-13, 5-11, 7-8, 0-2. Numbers of large caudal spines on T II-VIII as 18-26, 30-34, 28-34, 34-37, 46-53, 45-52, 44-50. Numbers of small caudal spines on T II-VIII as 18-26, 22-26, 27-41, 34-38, 31-40, 35-38, 18-20. Sternites V-VII (Fig. 6) each with an irregular row of short caudal spines. Pedes spurii A only on S VI, perhaps present on S VII as 1-2 minute spinules. Conjunctives II/III through V/VI each with 3-5 rows of thin spinules. Anal lobe without fringe. Apical spines absent. Anal macrosetae subequal, length 85-95.

LARVA — 4th INSTAR (n = 4)
Tan body with golden brown head capsule. Total length about 4050.

Head: length about 400, width about 280. Mouthparts and occipital margin dark brown. Mentum with 11 teeth (Figs. 13, 17). Median tooth pointed with 1st laterals adpressed; last lateral teeth reduced, mentum width: 85. Ventromental plate crescent shaped, thin, curving to base of mentum. Mandible (Fig. 12) sharply curved with three inner teeth; seta subdentalis short, truncate; seta interna with six or seven thin, regular, apically serrate filaments; mandible length 111. Epipharynx with SI (Fig. 14) apically bifid, SII simple; pecten epipharyngis with three blunt teeth, basal sclerite about as long as ungula. Premandible (Fig. 15) simple with mesal lobe; premandibular brush produced into a single large serrate seta; premandible length: 67. Maxilla (Fig. 11) with large palp and 6-7 smooth lacinial chaetae. Antenna (Fig. 10) 5-segmented with ring organ at base of segment I; blade with sclerotized base, length: 32; length of segments: 51:19:6:5:4; Lauterborn organs paired at of apex of II, length: 7; Segment I with two long basal lateral setae and mounted on short, sclerotized, spurred tubercle; AR: 1.48.

Body: length about 3600. Anal tubules (Fig. 16) much longer than posterior parapods. Procerci sclerotized and dark with large mesal spurs, each with five long (500) dark anal setae and two small lateral setae. Supraanal setae reduced. Posterior parapods each with 16 strong yellow claws. Long claws of anterior parapods serrate.
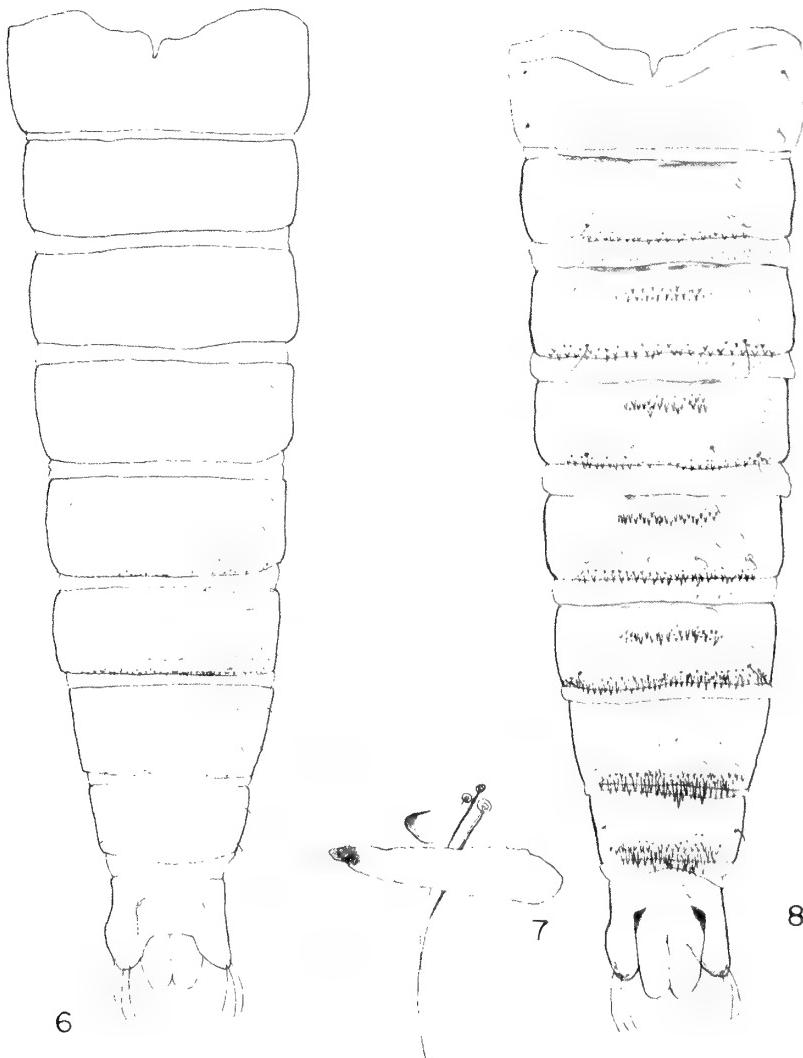
FIGS. 6-8.   *Paracricotopus mozleyi* n. sp. *Pupa* — 6. Sternites. — 7. Thoracic horn and precorneal setae. — 8. Tergites.

LARVA — 3rd INSTAR (n = 1)

As in the 4th instar but smaller with much darker head capsule. Total length about 1800. Median tooth of mentum relatively smaller. Length of antennal segments (Fig. 9) as 32:14:5:4:3.

Ecology: The specimens were all collected from a roadside vertical seep in the mountains of North Georgia. The open face of the outcrop faces southwest. Although samples were taken from all wet areas of the seep, live specimens were found only in colonies of the fragrant liverwort, *Conocephalum conicum.* Three species of plethodontid salamanders were present in large numbers in all damp areas of the outcrop. *Eurycea bislineata,* the southern two-lined salamander, inhabited the edges of the damp areas where rotten logs and sticks provided cover. *Desmognathus fuscus,* the dusky salamander, and *Desmognathus quadrimaculata,* the black-bellied salamander were actively crawling about and feeding in all wet areas. These last two species have enlarged hind legs and are often referred to as jumping salamanders because they are adept at leaping after low-flying insects. Several were observed as they captured adult chironomids. I collected two individuals of each species and examined their gut contents. The type specimen of *P. mozleyi* n. sp. was found in the foregut of a small dusky salamander along with adult tipulids and other larval chironomids. Most of a larval head was recovered from the gut of a small black-bellied salamander.

Larvae of *Hudsonimyia karelena* Roback were found in the company of *Paracricotopus mozleyi* n. sp. as were larvae of the genera *Tanytarsus, Corynoneura* and *Parametriocnemus.* The type specimens of *H. karelena* were found with the type specimens of *Paracricotopus glaber* in South Carolina (Roback 1979). The type localities of *P. mozleyi* n. sp. and *P. glaber* are about 100 km apart. Larvae of *P. mozleyi* n. sp. construct irregular trashy tubes. Their diet consists of diatoms, filamentous algae and detritus.

Distribution: Known only from the type locality.

Remarks: None of the life stages of either *P. glaber* or *P. mozleyi* will key readily in any published taxonomic reference. Because seeps occur in many scattered locations within the Appalachian Mountains, it is likely that other species of this genus remain undiscovered. To date, a total of eleven (three of *P. glaber* and eight of *P. mozleyi*) specimens of the genus *Paracricotopus* have been collected in North America.

Although the diagnostic characters presented here will separate the two species, if more specimens are ever collected, it might be determined that *P. mozleyi* is subspecific to *P. glaber.*

REFERENCES

ROBACK, S.S.   1979.   *Hudsonimyia karelena.* A new genus and species of Tanypodinae, Pentaneurini. Proc. Acad. Nat. Sci. Philadelphia 131:1-8.
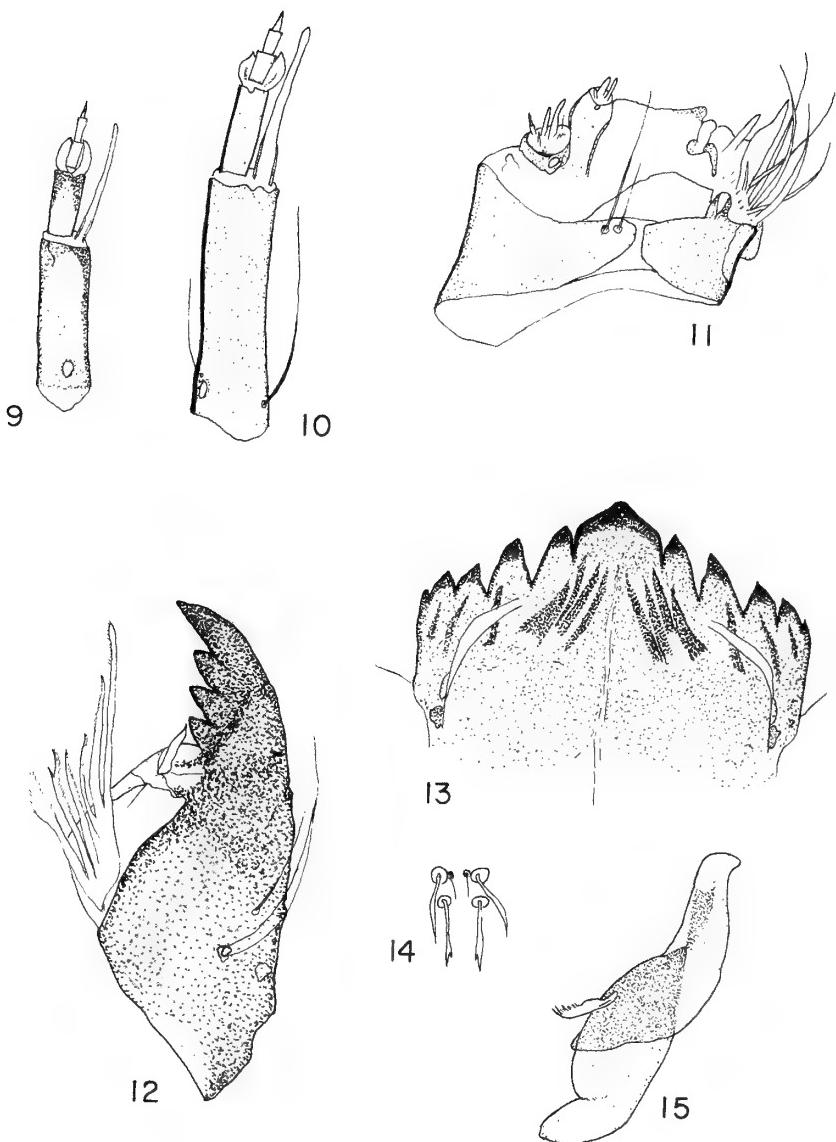
FIGS. 9-15. *Paracricotopus mozleyi* n. sp. *Larva* — 9. Antenna (3rd instar). — 10. Antenna. — 11. Maxilla. — 12. Mandible — 13. Mentum (new molt). — 14. Labral setae. — 15. Premandible.
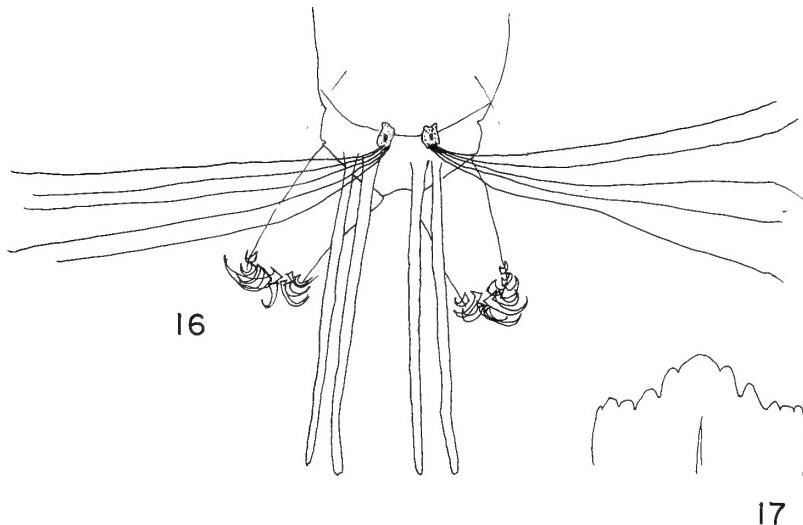
FIGS. 16-17. *Paracricotopus mozleyi* n. sp. *Larva* — 16. Posterior part of abdomen. — 17. Mentum showing normal wear.

SAETHER, O.A.   1980.   The females and immatures of *Paracricotopus* Thienemann and Harnisch, 1932, with the description of a new species (Diptera: Chironomidae). Aquatic Insects 2(3): 129-145.
_____. 1980a.   Glossary of chironomid morphology terminology (Diptera: Chironomidae). Ent. Scand. Suppl. 14:1-51.

Larval Esterases in Chironomus Thummi Kieff. and their Inhibition by Pesticides

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Abstract. — This paper reports an *in vitro* study of the esterase activity in *Chironomus thummi* larvae. A colorimetric investigation was conducted to study the kinetics of esterases, hydrolysing α and β naphthyl-acetate. Km values for α and β esterases resulted very similar (1.18×10^{-3}M and 1.134×10^{-4}M respectively). Esterase activity was also assayed in the presence of specific inhibitors, two carbamates (Eserine and Methomyl) and two organophosphates (Malathion and Dichlorvos) which, excepting Eserine, are commonly employed as pesticides. I_{50} values were 10^{-6}M for Dichlorvos and between 10^{-3} and 10^{-4}M for the other inhibitors. Enzyme kinetic studies in presence of these chemicals are outlined and discussed.

Introduction

Esterase inhibition by organophosphates and carbamates is well established: these chemicals are in fact commonly employed as pesticides, even if their insecticidal properties are questionably attributed to esterase inhibition only. These compounds have a short life in the environment, but because of the high concentrations of spray mixtures (about 10^{-3}M) and commonly used sprinkling frequencies, they have been found in their active form in fresh water bodies. For this reason, it is interesting to study the pesticide effect in aquatic organisms. *Chironomus thummi* was chosen because it has been shown to be very tolerant of polluted environments.

In this work we have studied the effect and the kind of inhibition of two organophosphates (Malathion and Dichlorvos) and two carbamates (Methomyl and Eserine) on α and β esterases of *Chironomus thummi* Kieff. larvae.

Materials and Methods

Fourth instar larvae were collected from Padua University Botanical Garden and, after identification, were stored in the freezer at $-30°$C.

The enzymatic tests were performed on homogenized pools according to Danford and Beardmore (1979) modified (Tallandini *et al.,* 1980), using α

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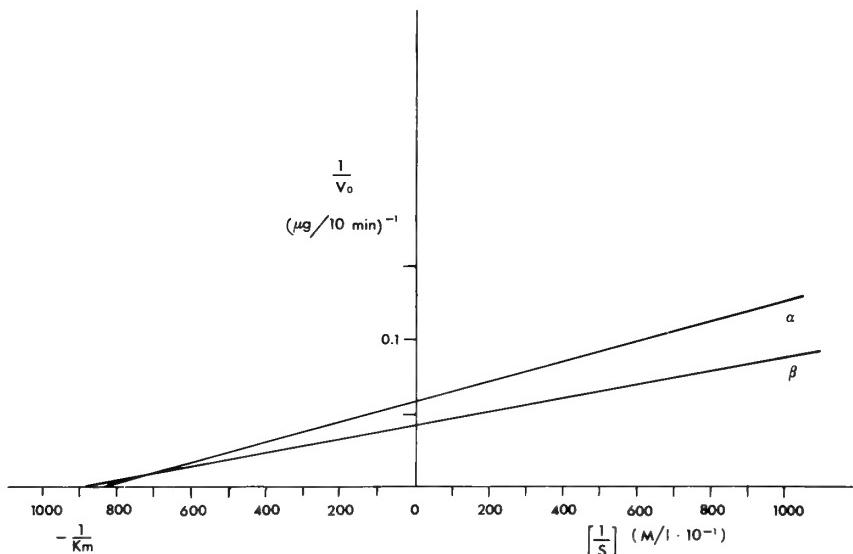
FIG. 1.   Lineweaver & Burk diagram for the reaction catalysed by α and β esterases at 25°C for 10 min.

and β naphthylacetate as substrates and Fast Red TR as dye. The hydrolisis was evaluated spectrophotometrically at 490 nm. The employed inhibitors were Malathion (from Cyanamid), Dichlorvos (from Ciba-Geigy), Methomyl (from Dupont) and Eserine (from Sigma). They were tested in serial dilutions from 10^{-2} to 10^{-9}M in sodium phosphate buffer (pH 6.5), with α and β naphthylacetate at constant concentration (2.6×10^{-3}M).

RESULTS

Fig. 1 shows the Lineweaver and Burk diagram of the α and β esterases; the Km values are 1.18×10^{-3}M for the α esterases and 1.134×10^{-3}M for the β esterases.

The inhibition by Malathion, Dichlorvos, Methomyl and Eserine (concentrations between 10^{-2}M and 10^{-9}M) is reported in Fig. 2. The I_{50} values are 10^{-6}M for Dichlorvos and between 10^{-4} and 10^{-3}M for the other inhibitors (Fig. 3). The reciprocal inhibition diagrams are shown in Figs. 4 and 5.
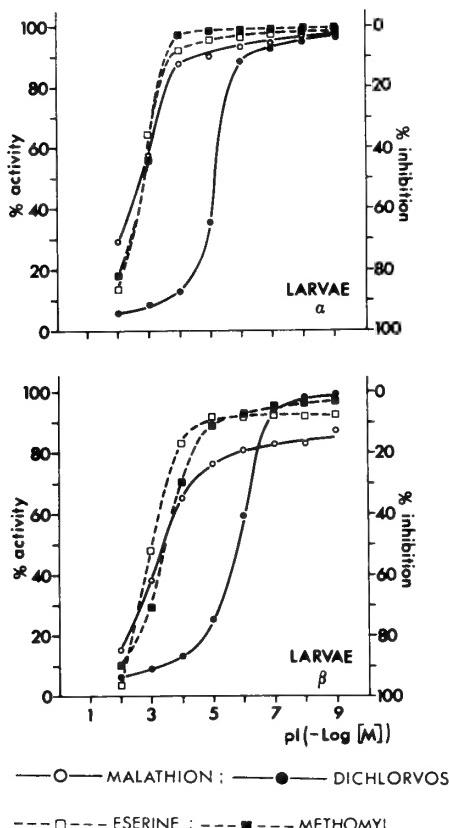
FIG. 2. Activity curves of α and β esterases in presence of the four inhibitors.

DISCUSSION

Our results clearly show that α and β esterases have very similar Km values, near to those reported by some authors for other Arthropods (Sudderuddin, 1973; Ho and Sudderuddin, 1976).

All the tested chemicals show a strong inhibitory activity and it is remarkable that the strongest inhibitor, also at low concentrations, is Dichlorvos ($I_{50} = 5.88 \times 10^{-6}$M for α esterases and $I_{50} = 1.77 \times 10^{-6}$M for β esterases) which, like all the chemicals studied, acts more on the β esterases than on the α esterases (Turchetto et al., 1981). Malathion, con-
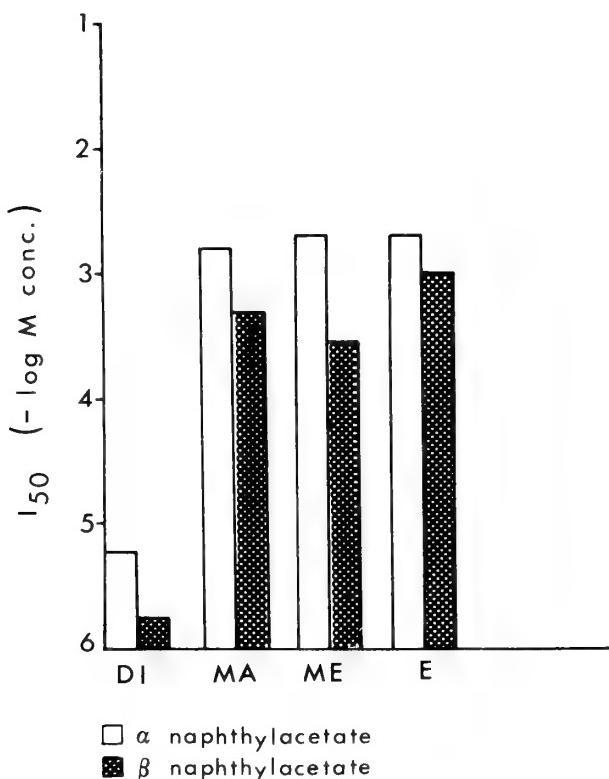
FIG. 3: Comparative I_{50} values for α and β esterases relative to the four inhibitors. Dl—Dichlorvos; MA—Malathion; ME—Methomyl; E-Eserine

versely, at the high concentrations shows less strength: this fact might depend both on the necessity of a previous metabolic desulfurization before linking with the enzymes and on a probable inactivation by carboxylesterases (Perry and Agosin, 1974; Dauterman and Hodgson, 1978). The two carbamates show a very similar inhibition.

The kind of inhibition is difficult to evaluate: in certain cases it is clearly competitive (Eserine with β esterases) or incompetitive (Methomyl with α esterases) or noncompetitive (Dichlorvos and Eserine with α and Malathion with β esterases). The other results are difficult to evaluate because we have employed pools of various esterases which may be present as molecular aggregates or as unique molecules with a multiple number of sites (Hipps and Nelson, 1974) and therefore may interact with the inhibitors in different ways. In this respect, the data previously reported are not exhaustive.
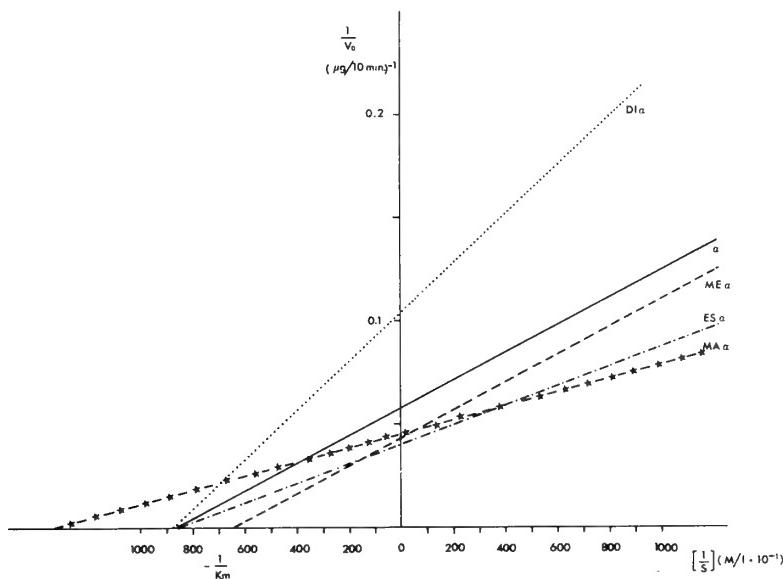
FIG. 4. Lineweaver & Burke diagram for α esterases with the inhibitors (Di = Dichlorvos, Ma = Malathion, Me = Methoyml, Es = Eserine).

REFERENCES

DANFORD, N.D. AND J.A. BEARDMORE. 1979. Biochemical properties of esterases-6 in *Drosophila melanogaster*. Biochem. Genetics 17:1-22.

DAUTERMAN, W.C. AND E. HODGSON. 1978. Detoxication mechanisms in insects. *In:* "Biochemistry of Insects," Rockestein M. ed., Acad. Press, London, 541-577.

HIPPS, P.P. AND D.R. NELSON. 1974. Esterases from the midgut and gastric caecum of the American Cockroach, *Periplaneta americana* (L.), isolation and caraterization. Biochem. Biophys. Acta, 341:421-436.

HO, S.H. AND K.I. SUDDERUDDIN. 1976. An *in vitro* study of the non-specific esterases of the melon fly, *Dacus cucurbitae* coq. and their reactions with organophosphate and carbamate compounds. Comp. Biochem. Physiol. 54C:95-97.

PERRY, A.S. AND M. AGOSIN. 1974. The physiology of insecticide resistance by insects. *In:* "The Physiology of Insecta," Rockestein M. ed., Acad. Press, London, 2nd ed., 6:3-121.

SUDDERUDDIN, K.I. 1973. An *in vitro* study of esterase, hydrolysing non-specific substrates, of an OP-resistant strain of the green peach aphid, *Myzus persicae* (Sulz.). Comp. Biochem. Physiol. 44B:1067-1076.

TALLANDINI, L., M. TURCHETTO AND U. FERRARESE. 1980. Esterase evidentiation and characterization in the course of ontogenesis in *Chironomus thummi* Kieff. *In:* "Chironomidae," D.A. Murray, ed., Pergamon Press, Oxford, pp. 35-41.

TURCHETTO, M., A. DIOTTO AND L. TALLANDINI.   1981.   *In vitro* study of esterase inhibition in the midge *Chironomus thummi* Kieff. (Diptera, Chironomidae): 1. Organophosphates and Carbamates. Boll. Zool. 48:335-339.
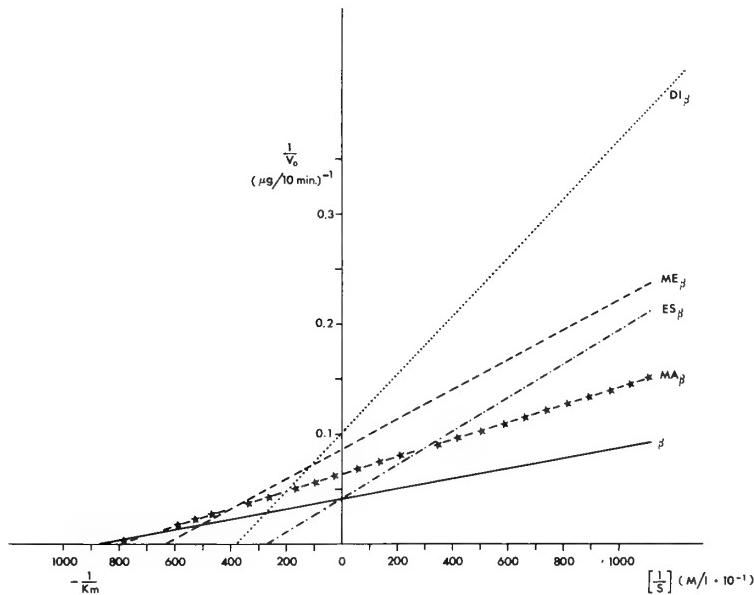
FIG. 5.   Lineweaver & Burk diagram for β esterases with the inhibitors (Di = Dichlorvos, Ma = Malathion, Me = Methomyl, Es = Eserine).

Diel Periodicity in Adult Emergence of Chironomids (Diptera: Chironomidae) in an Oligotrophic Lake

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Abstract. — The diel periodicity in adult emergence of nine species of chironomids from an oligotrophic, temperate lake was observed. *Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris, Stempellina ranota,* and *Stempellina rodesta* exhibited a diurnal pattern of emergence. *Pagastiella ostansa, Tanytarsus flavellus, Tanytarsus trilobus,* and *Zalutschia obsepta* exhibited a crepuscular emergence. *Cryptotendipes casuarius* emerged nocturnally. No correlation was evident between bottom water temperatures and the peak of emergence in any of these species. A positive correlation was evident between the change in light intensity from light to darkness and the peak of emergence in those species exhibiting crepuscular or nocturnal emergence patterns. No pattern of protandry was exhibited by any of the species observed. Males emerged in greater numbers than females in *Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris, Stempellina ranota, Stempellina rodesta,* and *Zalutschia obsepta,* and females emerged in greater numbers than males in *Cryptotendipes casuarius, Pagastiella ostansa, Tanytarsus flavellus,* and *Tanytarsus trilobus.*

Introduction

The diel periodicity of adult emergence in chironomids has been studied for a variety of species in the arctic (Danks & Oliver 1972; Kureck 1966; Oliver 1968, 1971; Remmert 1965), subarctic (Koskinen 1968; Lindeberg 1958), temperate (Ali 1980; Ali & Mulla 1979; Miller 1941; Morgan 1958; Morgan & Waddell 1961; Mundie 1959; Nielsen 1962a, 1962b; Scott & Opdyke 1941; Wool & Kugler 1969), subtropic (Lewis 1957), and marine and brackish-water environments (Caspers 1951; Neumann 1971; Palmen 1955, 1956a, 1956b [1958], 1958; Tokunaga 1932, 1934), as well as experimentally (Englemann & Shappirio 1965; Fischer & Rosin 1968; Phillipp 1938; Remmert 1955a, 1955b). In general, species of chironomids have distinct diurnal, crepuscular, or nocturnal patterns of emergence although occasionally adults may emerge throughout the day with no distinct peak of abundance. Some species are bivoltine. Of particular interest have been the effects of exogenous factors in initiating and regulating the pattern of diel emergence, such as temperature, changes in light intensity, and lunar periodicity.

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As part of an ecological study of the Chironomidae of Costello Lake, Algonquin Provincial Park, Ontario, Canada, the diel periodicity of adult emergence was determined for nine species of chironomids, *Bryophaenocladius flavoscutellatus* (Malloch), *Cladotanytarsus viridiventris* (Malloch), *Cryptotendipes casuarius* (Townes), *Pagastiella ostansa* (Webb), *Stempellina ranota* Webb, *Stempellina rodesta* Webb, *Tanytarsus flavellus* (Zetterstedt), *Tanytarsus trilobus* Webb, and *Zalutschia obsepta* (Webb), from the littoral and sublittoral zones. Attempts to assess the diel periodicity of adult emergence from the profundal zone were unsuccessful, because insufficient numbers of adults were collected to determine any pattern. Emerging adults were collected from the time the lake was ice free (5 May 1965) until the emergence of adults ended (11 October 1965). Of particular interest were the effects of bottom water temperatures and changes in light intensity on the pattern of diel emergence of spring- (5 May-15 June), summer- (16 June-15 August), and autumn- (16 August-11 October) emerging species, on those species having two generations of adults per year, and on the quantitative differences between males and females.

Costello Lake (Fig. 1) is a small oligotrophic lake located (45° 35' N, 78°20' W) in the Precambrian Shield in Algonquin Provincial Park, Ontario. It covers an area of 39 ha, with a maximum depth of 19 m. The lake

COSTELLO LAKE

DEPTH IN METERS
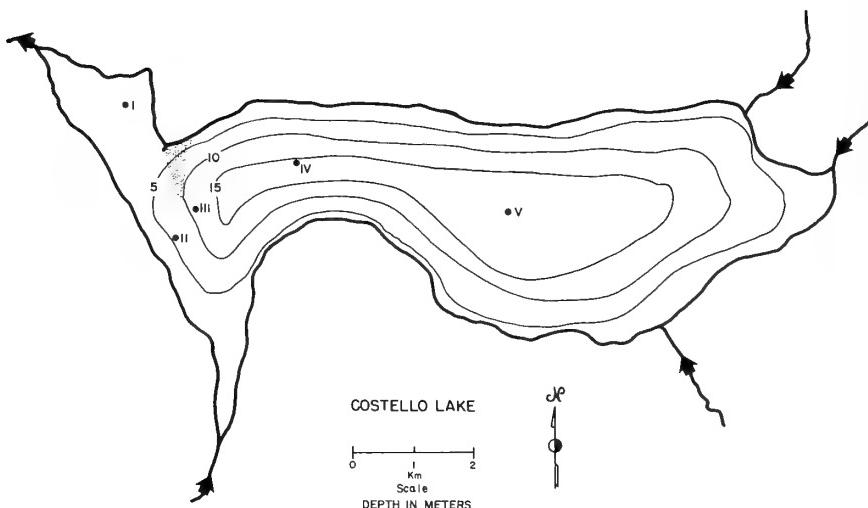
FIG. 1.   Costello Lake, Algonquin Provincial Park, Ontario. Collecting stations are indicated in Roman numerals.

has two small bays located in the southwest and northwest corners. The northwest bay is 3 m or less in depth and supports an abundance of aquatic macrophytes (*Nymphaea odorata, Vallisneria americana, Sagittaria latifolia, Potamogeton natans, Dulichium arundinaceum, Nuphar* sp., and *Brasenia schreberi*). The remainder of the lake has only a narrow fringe of aquatic macrophytes. To a depth of 7-9 m the bottom substrate consists of fine silt, with the exception of a narrow sandbar at the southeast corner of the northwest bay. Below 7-9 m the bottom substrate consists of ooze. Costello Lake stratifies thermally during the summer, and hypoxial conditions occur in the deeper areas of the profundal zone from early August until autumn turnover.

METHODS

Diel emergence patterns were determined from adults collected in three 1-m² surface emergence traps (Fig. 2) anchored over a depth of 1.5 m in the littoral zone of the northwest bay (Station I) and, on three occasions, over a depth of 5 m in the sublittoral zone at the west end of the lake (Station II). Adult chironomids aggregated at the peak of each trap and were easily
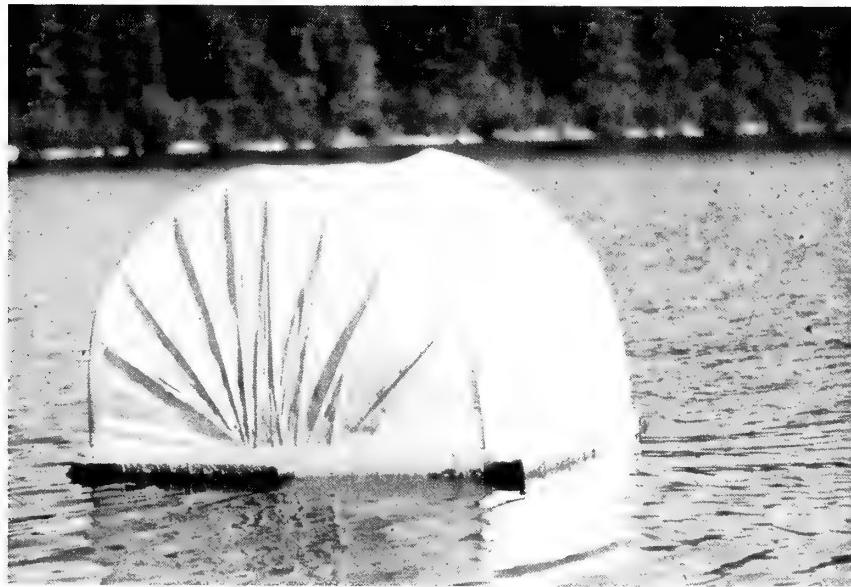
Fig. 2.   Surface emergence trap.

aspirated while inclining the trap to one side. During each study period the adult chironomids were removed from the three traps every hour, generally beginning at 0600 (EST) hours, for 1-3 days. Measurements of water temperature and light intensity at the lake bottom were taken each time the emergence traps were examined. Bottom water temperatures were measured with a thermistor thermometer. Light penetration was measured at the lake bottom with a Weston photronic cell (spectral sensitivity 430-700 nm) mounted in a brass waterproof casing and fitted with a translucent parabolic dome to concentrate light from above onto the photoelectric cell. Light intensity was measured as a percentage of full surface sunlight taken at noon on 12 June 1965. The period of twilight was considered to be that period when the light intensity at the lake bottom fell below 1.0 percent.

Results and Discussion

1. *Zalutschia obsepta* was observed at Station I on 10-11 May, with adults emerging from 1100-2100 hours. Ninety percent of these adults emerged from 1800-2000 hours, with the peak emergence (Fig. 3) from 1800-1900 hours, 1.5 to 0.5 hr before sunset, but at a time when no detectable light was measured at the lake bottom. No adults emerged after 2100 hours. Fifty-six males and 24 females emerged (ratio 2.3:1). Bottom water temperatures ranged from 7.6 to 8.6 °C and were declining during the peak emergence.

Zalutschia obsepta began emerging as soon as Costello Lake became icefree on 5 May 1965. Its crepuscular pattern of diel periodicity was a distinct exception to the expected pattern of emergence. Generally, early spring-emerging species of chironomids are expected to emerge during mid-day (Morgan & Waddell 1961), as low night temperatures are considered a disadvantage to emergence (Morgan & Waddell 1961).

2. *Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris,* and *Stempellina ranota* were observed at Station I on 16-17 May. All three species reached their peak emergence (Fig. 4) during the morning from 0900-1000 hours, 4-5 hr after sunrise. No adults emerged after 1800 hours. Bottom water temperatures on 16 May ranged from 9.2 to 11.7 °C and on 17 May from 9.4 to 11.1 °C, but were increasing during the peak emergence on 16 May and declining during the peak of emergence on 17 May.

Bryophaenocladius flavoscutellatus emerged from 0700 to 1700 hours on 16 May and from 0700 to 1800 hours on 17 May. On 16 May 322 males and 81 females emerged (ratio 4.0:1), and on 17 May 269 males and 74 females emerged (ratio 3.6:1).

Cladotanytarsus viridiventris emerged from 0600 to 1800 hours on 16 May and from 0600 to 1600 hours on 17 May. On 16 May, 290 males and 55
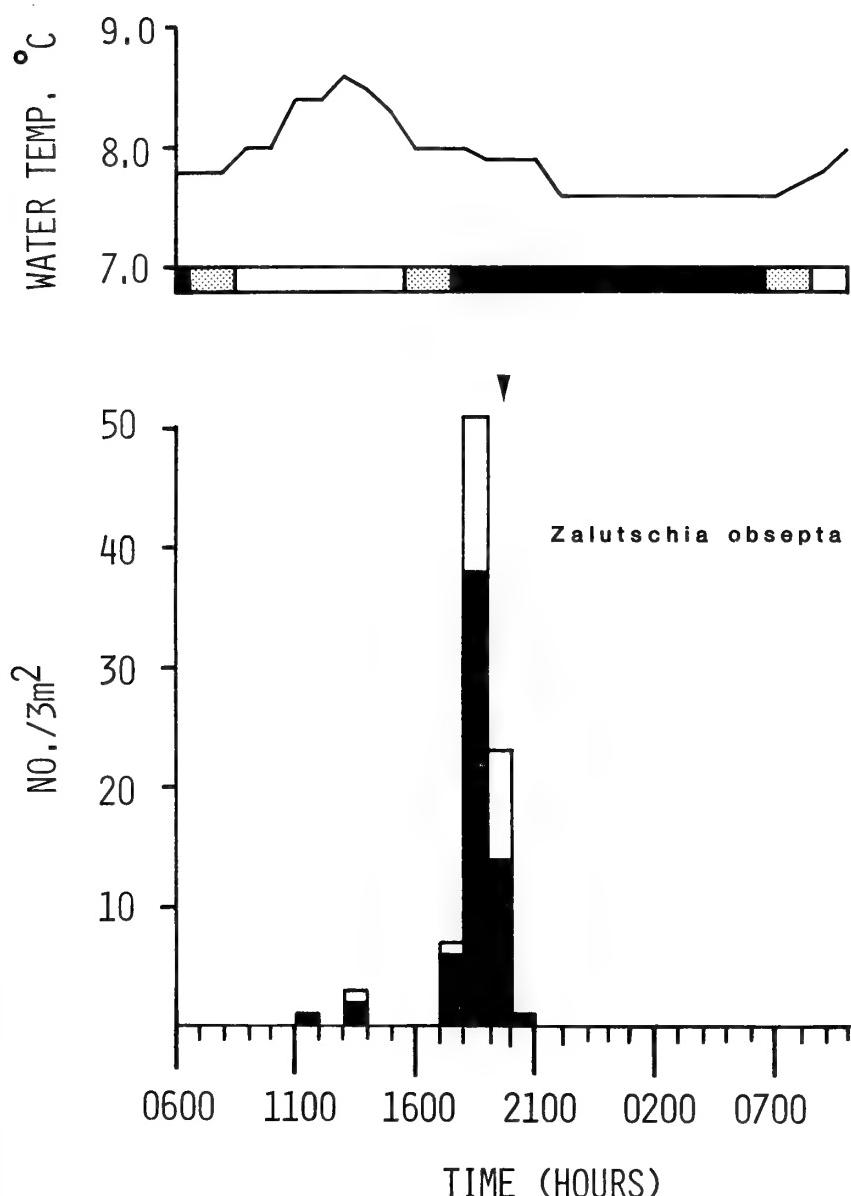
FIG. 3. *Zalutschia obsepta*. Diel periodicity of adult emergence from the littoral zone of Costello Lake, 10-11 May 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.

females emerged (ratio 5.3:1), and on 17 May 338 males and 100 females emerged (ratio 3.4:1).

Stempellina ranota emerged from 0600 to 1700 hours on 16 May and from 0500 to 1800 hours on 17 May. On 16 May, 278 males and 88 females emerged (ratio 3.2:1), and on 17 May, 338 males and 84 females emerged (ratio 4.0:1).

Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris, and *Stempellina ranota* followed the expected pattern of diel emergence for early spring-emerging chironomids (Morgan & Waddell 1961). No distinct correlation was evident to indicate that water temperature was the exogenous cue initiating the emergence of these species, as was noted for arctic species (Danks & Oliver 1972; Kureck 1966; Oliver 1968, 1971; Remmert 1965).

3. *Tanytarsus trilobus* was a bivoltine species in Costello Lake, and was observed at Station I on five occasions, twice during the spring and three times during the late summer and early autumn. On 31 May-1 June, *T. trilobus* emerged from 1000 to 2400 hours with the peak emergence from 1900 to 2000 hours (Fig. 5A), 1 hr before sunset. No adults emerged after 2400 hours. Sixty-five females and 57 males emerged (ratio 1.1:1). Bottom water temperatures ranged from 12.5 to 13.9 °C and were generally static during the peak emergence.

On 6-7 June, *T. trilobus* emerged from 1200 to 0600 hours, with the peak emergence from 1900 to 2000 hours (Fig. 5B), 1 hr before sunset. Adults emerged at low levels throughout the night. One hundred and twenty-two females and 91 males emerged (ratio 1.3:1). Bottom water temperatures ranged from 17.1 to 18.2 °C and were static during the peak emergence.

On 19-20 August, *T. trilobus* emerged from 1400 to 2200 hours, with the peak emergence from 2000 to 2100 hours (Fig. 5C), 0.75-1.75 hr after sunset. No adults emerged after 2200 hours. Fifty-five females and 49 males emerged (ratio 1.1:1). Bottom water temperatures ranged from 17.9 to 21.1 °C and were declining during the peak emergence.

On 30-31 August, *T. trilobus* emerged from 0700 to 2400 hours, with the peak emergence from 2000 to 2100 hours (Fig. 5D), 1-2 hr after sunset. No adults emerged after 2400 hours. Forty-six females and 36 males emerged (ratio 1.3:1). Bottom water temperatures ranged from 15.0 to 16.9 °C and were declining during the peak emergence.

On 11-12 September, *T. trilobus* emerged from 1500 to 2300 hours, with scattered emergence throughout the morning and afternoon. The peak emergence occurred from 1900 to 2000 hours (Fig. 5E), 1 hr after sunset. No adults emerged after 2300 hours. Forty-eight females and 38 males emerged (ratio 1.3:1). Bottom water temperatures ranged from 16.0 to 17.6 °C and were declining during the peak emergence.
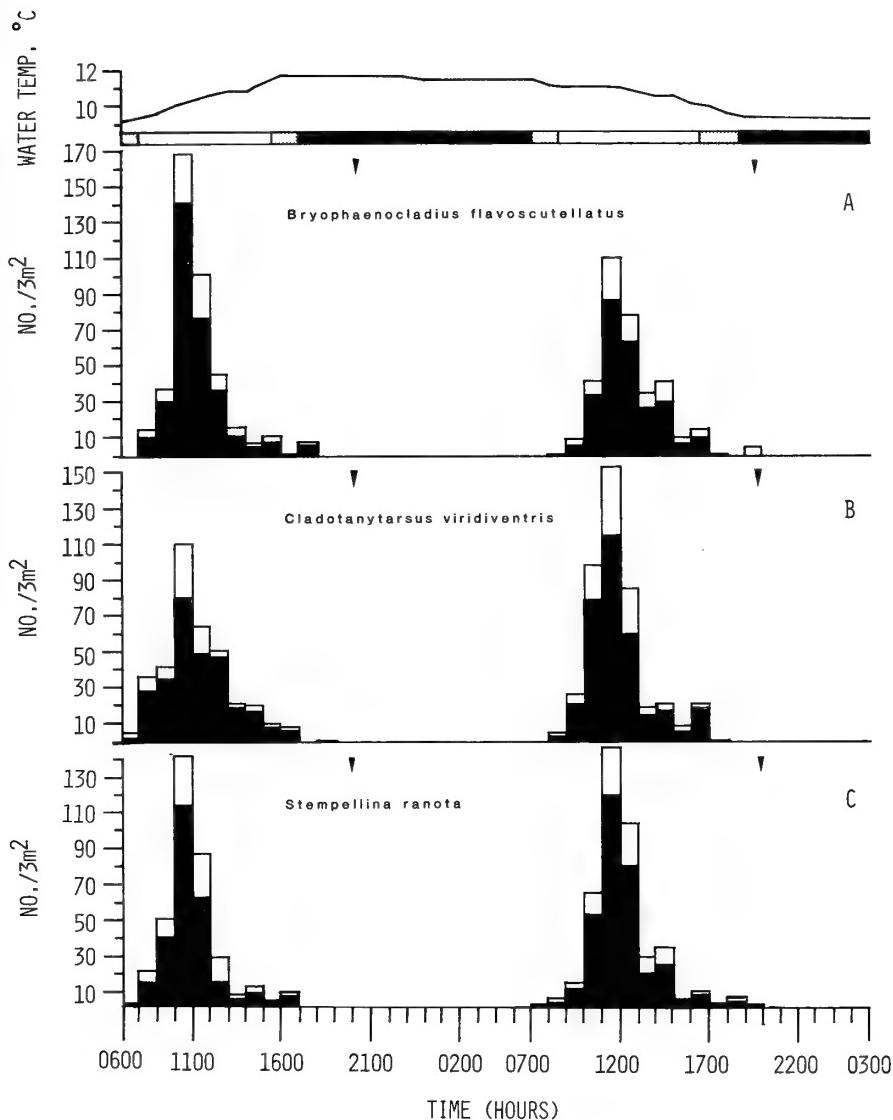
FIG. 4. *Bryophaenocladius flavoscutellatus* (A), *Cladotanytarsus viridiventris* (B), and *Stempellina ranota* (C). Diel periodicity of adult emergence from the littoral zone of Costello Lake, 16-17 May 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.

In the spring generation of *T. trilobus,* the peak emergence occurred from 1900 to 2000 hours, the hour before sunset. The second generation, emerging in late summer and early autumn, peaked at 2000-2100 hours, 1 hour later than that observed in the spring generation, yet the time of sunset in late summer and early autumn was 45 min to 1 hr earlier than sunset during the spring studies. The peak emergence in September occurred from 1900 to 2000 hours, the same as in the two spring studies, but sunset in September was 1 hr and 15 min earlier than it was during the spring studies. Morgan & Waddell (1961) observed that the peak of emergence in the second generation of *Chironomus (Cryptochironomus) krusemani* Goetghbuer occurred 2 hours earlier than that of the spring generation but corresponded to the change in the time of sunset between June and August. Palmen (1955, 1956a, 1956b [1958], 1958) noted a similar shift in the peak of emergence relative to the earlier occurrence of sunset during the second generations of *Chironomus halophilus* Kieffer, *Lenzia flavipes* De Geer, *Microtendipes pedellus* De Geer, *Monotanytarsus inopertus* (Walker), *Polypedilum nuberculosum* De Geer, and *Tanytarsus heusdensis* Goetghbuer. Caspers (1951) observed that emergence in *Clunio marinus* Haliday coincided with the local time of sunset when pupae from Helgoland were transferred to Varna on the Black Sea (a difference of 20° longitude), indicating that emergence was regulated by exogenous factors, in particular the change in light intensity from light to darkness.

In the second generation of *T. trilobus* the emergence observed on 11-12 September showed a 1-hour shift in peak emergence corresponding to the earlier occurrence of sunset.

Morgan & Waddell (1961) observed a change in the peak emergence of *Microtendipes chloris* Meigen from midday in the March-April generation to nocturnal in the June-July generation. Fischer & Rosin (1968) observed in *Chironomus nuditarsis* Strenzke that the time of emergence in relation to light-dark changes can be modified by temperature levels. At 18 °C, *C. nuditarsis* normally emerged at dusk, but when temperatures were lowered to 13 °C, peak emergence occurred at dawn. Phillipp (1938, Fig. 5), in an experimental study of diel emergence in *Chironomus thummi* Kieffer, showed that peak emergence generally occurred earlier as water temperatures dropped.

FIG. 5.   *Tanytarsus trilobus.* Diel periodicity of adult emergence from the littoral zone of Costello Lake, 31 May — 1 June (A), 6-7 June (B), 19-20 August (C), 30-31 August (D), and 11-12 September (E) 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.
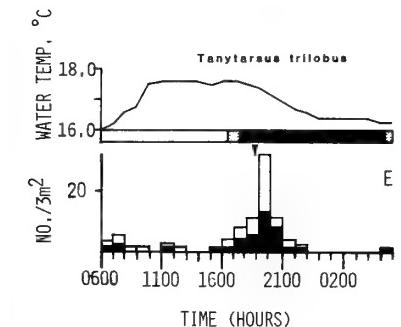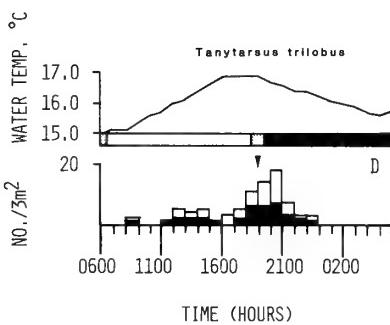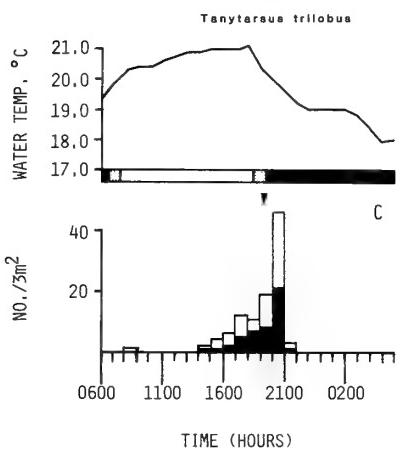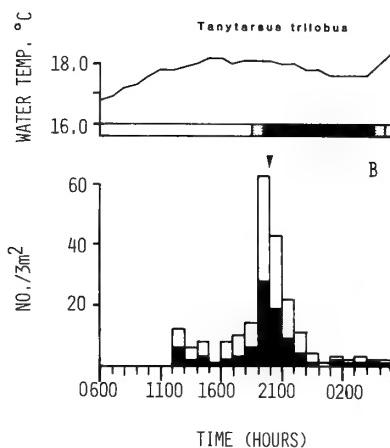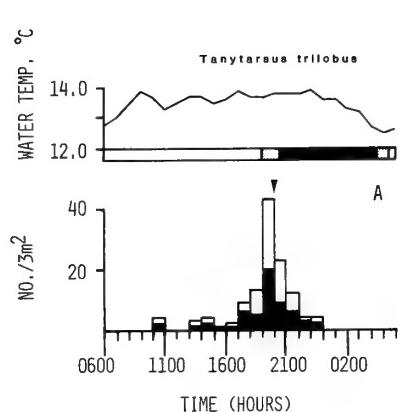
In Costello Lake bottom water temperatures during the two spring study periods ranged from 12.5 to 13.9 °C and from 17.1 to 18.2 °C, respectively, with the peak emergence of *T. trilobus* at 1900-2000 hours. During the three studies on the second generation of *T. trilobus* bottom water temperatures ranged from 17.9 to 21.1, 15.0 to 16.9, and 16.0 to 17.6 °C, respectively, with the peak emergence at 2000 to 2100 hours, 2000 to 2100 hours, and 1900 to 2000 hours, respectively. During the 30-31 August and 11-12 September studies, the peak emergence varied by 1 hour, yet the bottom water temperatures were nearly the same. It is evident that variation in water temperatures is not correlated with variations in peak emergence between spring and autumn generations.

4. *Cryptotendipes casuarius* was observed at Station II on 12-15 July, with adults emerging from 2100 to 2400, 2000 to 0100, and 2100 to 2400 hours, respectively, during each of three nights. The peak emergence occurred from 2200 to 2300 hours during each night (Fig. 6), with no emergence after 0100 hours. On 12 July, 64 females and 24 males emerged (ratio 2.7:1); on 13 July, 29 females and 14 males emerged (ratio 2.1:1); and on 14 July, 45 females and 13 males emerged (ratio 3.5:1). Bottom water temperatures on 12 July ranged from 15.2 to 18.0 °C; on 13 July, from 16.3 to 18.5 °C;
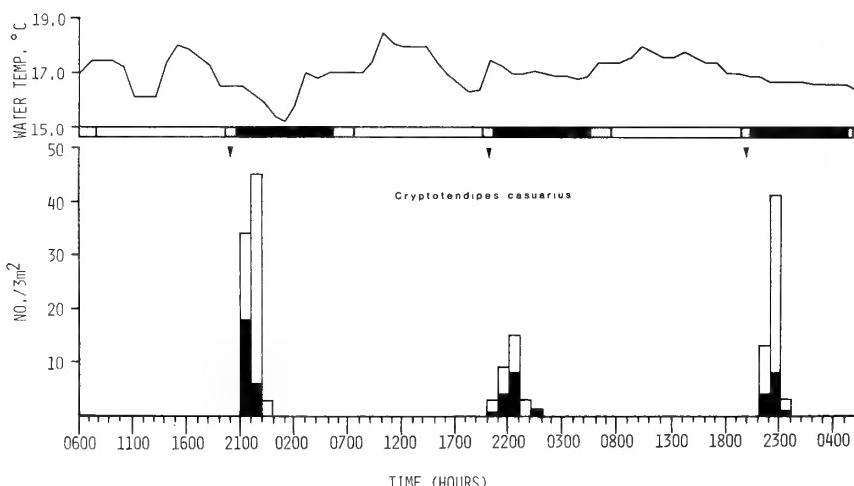
Fig. 6. *Cryptotendipes casuarius*. Diel peroidicity of adult emergence from the sublittoral zone of Costello Lake, 12-15 July 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.

and on 14 July, from 16.4 to 18.0 °C, and were declining on all three nights during the peak emergence.

C. casuarius was a summer-emerging species from the sublittoral zone of Costello Lake. It was the only species exhibiting a nocturnal pattern of emergence similar to those observed by Ali (1980), Ali & Mulla (1979), Miller (1941), Morgan & Waddell (1961), and Mundie (1959) for other summer-emerging species.

5. *Stempellina rodesta* was a summer-emerging species in Costello Lake. At Station I, on 16-17 July, adults emerged continuously during the daylight hours, increasing to a peak from 1900 to 2000 hours (Fig. 7), 1 hr before to sunset. Emergence then dissipated rapidly following sunset, with no adults emerging after 2100 hours. Two hundred and forty-seven males and 81 females emerged (ratio 3.0:1). Bottom water temperatures ranged from 19.0 to 20.1 °C, and were beginning to decline during the peak emergence.

Stempellina rodesta was a summer-emerging species in Costello Lake, but it emerged during the daylight hours in contrast with the general crepuscular pattern observed for other summer-emerging species (Ali 1980; Ali & Mulla 1979; Morgan 1958; Morgan & Waddell 1961; Nielsen 1962a, 1962b; Palmen 1955, 1956a, 1956b [1958], 1958; Scott & Opdyke 1941, Tokunaga 1932, 1934). The pattern for *S. rodesta* was more characteristic of spring-emerging (Morgan & Waddell 1961) or arctic species (Danks & Oliver 1972; Kureck 1966; Oliver 1968, 1971; Remmert 1965).

6. *Pagastiella ostansa* was observed at Station I in early August and at Station II in late July and mid-August. On 28 July, at Station II, *P. ostansa* emerged from 1600 to 2400 hours, and on 29 July, from 1600 to 2300 hours, with the peak emergence on both nights from 1900 to 2000 hours (Fig. 8A), 45 min before to 15 min after sunset. No adults emerged after 2400 hours. On 28 July, 83 females and 58 males emerged (ratio 1.4:1), and on 29 July, 92 females and 52 males emerged (ratio 1.8:1). Bottom water temperatures on 28 July ranged from 18.0 to 19.7 °C, on 29 July from 18.4 to 19.8 °C, and were declining during the peak emergence.

On 4 August, at Station I, *P. ostansa* emerged from 1700 to 2300 hours, and on 5 August from 1600 to 2300 hours, with the peak emergence from 1900 to 2000 hours (Fig. 8B), 45 min before to 15 min after sunset. No adults emerged after 2300 hours. On 4 August, 88 females and 58 males emerged (ratio 1.5:1), and on 5 August 101 females and 85 males emerged (ratio 1.2:1). Bottom water temperatures on 4 August ranged from 18.6 to 19.9 °C, on 5 August from 19.0 to 19.4 °C, and were declining or static during the peak emergence.

On 18 and 19 August, at Station II, *P. ostansa* emerged from 1700 to

2100 hours, with the peak emergence from 1900 to 2000 hours (Fig. 8C), 15 min before to 45 min after sunset. No adults emerged after 2100 hours. On 18 August, 36 females and 30 males emerged (ratio 1.2:1), and on 19 August, 32 females and 26 males emerged (ratio 1.2:1). Bottom water temperatures on 18 August ranged from 15.2 to 18.0 °C, on 19 August from 14.2 to 16.8 °C, and were declining during the peak emergence.

P. ostansa was a summer-emerging species in Costello Lake with a crepuscular pattern of emergence similar to those observed by Ali (1980). Ali & Mulla (1979), Morgan (1958), Morgan & Waddell (1961), Nielsen (1962a, 1962b), Palmen (1955, 1956a, 1956b [1958], 1958), Scott & Opdyke (1941), and Tokunaga (1932, 1934) for other summer-emerging species. No difference was exhibited in diel periodicity in adults emerging from the sublittoral (28-29 July) or littoral zones (4-5 August).

7. *Tanytarsus flavellus* was observed at Station I during mid-August and mid-September. On 19 August, *Tanytarsus flavellus* emerged from 1700 to 2200 hours, with the peak emergence from 2000 to 2100 hours (Fig. 9A), 45 min to 1.75 hr after sunset. No adults emerged after 2200 hours. Thirty-three females and 31 males emerged (ratio 1.1:1). Bottom water temperatures ranged from 17.9 to 21.0 °C, and were declining during the peak emergence.

On 11 September, *T. flavellus* emerged from 1800 to 2200 hours, with the peak emergence from 1900 to 2000 hours (Fig. 9B), 15 min to 1.25 hr after sunset. No adults emerged after 2200 hours. Twenty-seven females and 27 males emerged during this study. Bottom water temperatures ranged from 16.0 to 17.6 °C, and were declining during the peak emergence.

T. flavellus was a late summer-emerging species in Costello Lake with a crepuscular pattern of emergence. The peak emergence in September occurred 1 hour earlier than in August. This correlated with the earlier occurrence of sunset in September although the actual difference in time was only 30 min. A similar trend was observed in the August and September emergences of *Tanytarsus trilobus*.

Miller (1941), in an earlier study of Costello Lake, noted that the diel emergence of chironomids in mid-July ". . . occurred between the hours of four and seven A.M., a time of low light intensity and minimum temperature. . . ." Although Miller did not identify his species, none of

FIG. 7.   *Stempellina rodesta*. Diel periodicity of adult emergence from the littoral zone of Costello Lake, 16-17 July 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.

Stempellina rodesta
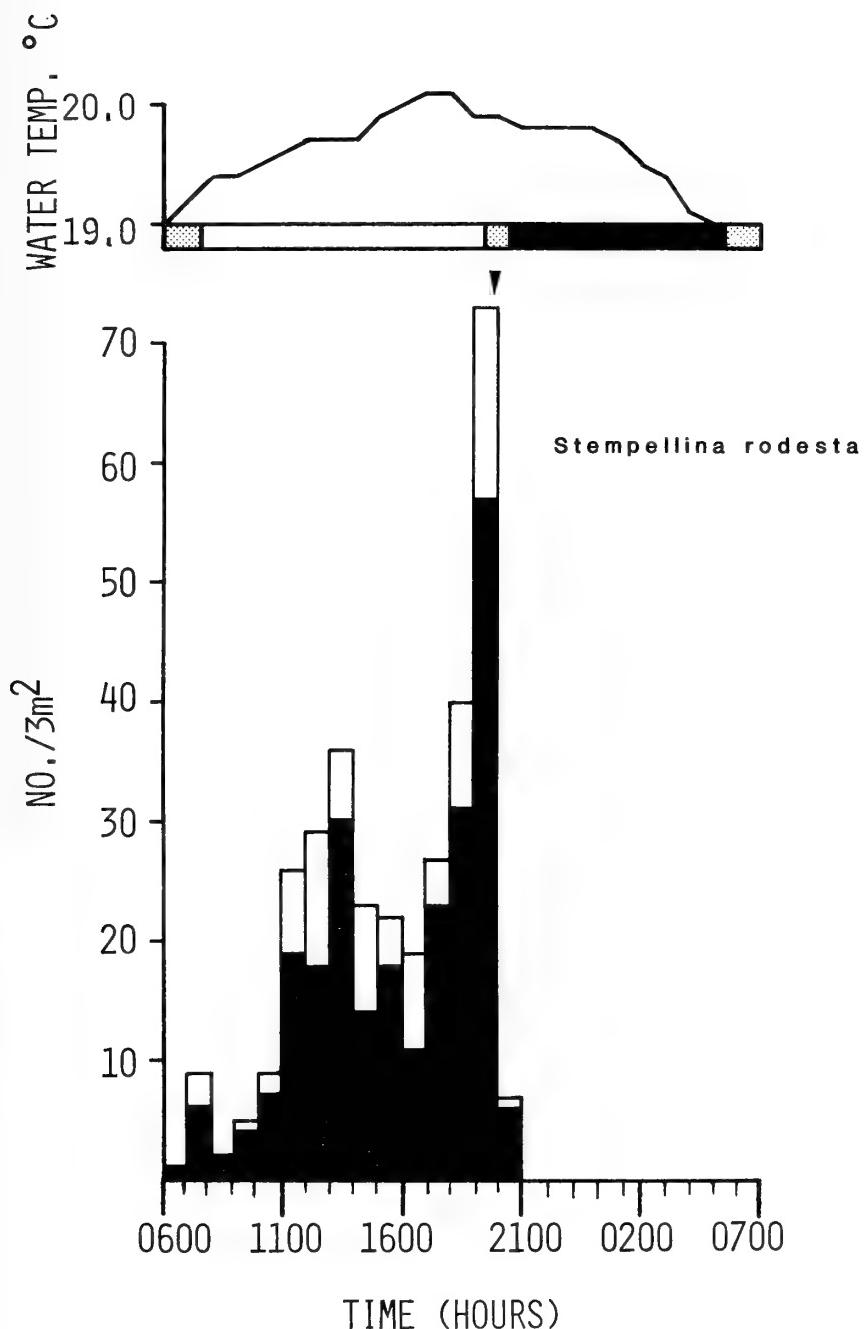
the chironomids that I examined during 12 collecting periods exhibited any trend toward emerging near sunrise.

During this entire study of diel emergence, no pattern of diel protandry was exhibited by any of the species examined, although in *Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris, Stempellina ranota, S. rodesta,* and *Zalutschia obsepta* males emerged in distinctly greater numbers than females (ratio 2.3-4.0:1). In *Cryptotendipes casuarius,* more females than males emerged (ration 2.1-3.5:1). In *Pagastiella ostansa, Tanytarsus flavellus* and *T. trilobus* females emerged in slightly larger numbers than males (ratio 1.0-1.8:1).

Summary

The diel periodicity of adult emergence in nine species of chironomids from an oligotrophic lake were observed. *Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris, Stempellina ranota,* and *S. rodestus* had a diurnal pattern of emergence. *Pagastiella ostansa, Tanytarsus flavellus, T. trilobus,* and *Zalutschia obsepta,* had a crepuscular pattern of emergence. *Cryptotendipes casuarius* had a nocturnal pattern of emergence.

No correlation was evident between bottom water temperatures and peaks of emergence.

A correlation was evident between the change from light to darkness and the peak emergence in those species exhibiting crepuscular and nocturnal patterns of emergence. In the bivoltine species, *Tanytarsus trilobus,* the peak emergence in the spring generation occurred during the hour before sunset, yet in the second generation the peak emergence occurred during the hour after sunset. This variation could not be correlated with the time of sunset occurring earlier in the summer than in the spring.

No diel pattern of protandry was exhibited by any of the species observed. In *Bryophaenocladius flavoscutellatus, Cladotanytarsus viridiventris, Stempellina ranota, S. rodesta,* and *Zalutschia obsepta* males emerged in distinctly greater numbers than females. In *Cryptotendipes casuarius* females emerged in greater numbers than males. In *Pagastiella ostansa, Tanytarsus flavellus,* and *T. trilobus* females emerged in slightly greater numbers than males.

Fig. 8.   *Pagastiella ostansa.* Diel periodicity of adult emergence from the sublittoral zone, 28-29 July (A) and 18-19 August (C), and from the littoral zone, 4-5 August (B), of Costello Lake 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.
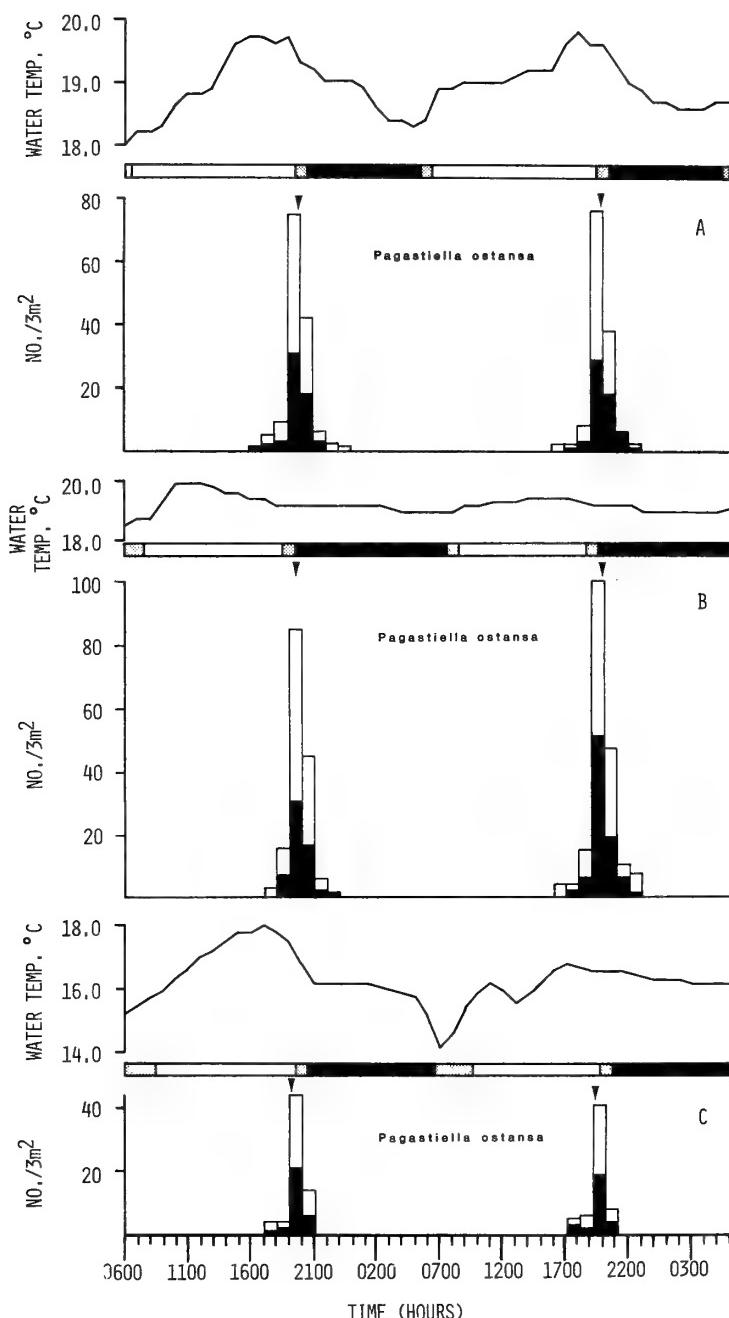
LITERATURE CITED

ALI, A.   1980.   Diel adult eclosion periodicity of nuisance chironomid midges of central Florida. Environ. Entomol. 9:365-370.

_____ AND M. S. MULLA.   1979.   Diel periodicity of eclosion of adult chironomid midges in a residential-recreational lake. Mosq. News 39:360-364.

CASPERS, H.   1951.   Rhythmische Erscheinungen in der Fortpflanzung von *Clunio marinus* (Dipt., Chiron.) und das Problem der lunaren Periodizitat. Arch. Hydrobiol., Suppl. 18:415-594.

DANKS, H. V. AND D. R. OLIVER.   1972.   Diel periodicities of emergence of some high Arctic Chironomidae (Diptera). Can. Entomol. 104:903-916.

ENGLEMANN, W. AND D. G. SHAPPIRIO.   1965.   Photoperiodic control of the maintenance and termination of larval diapause in *Chironomus tentans*. Nature 207:548-549.

FISCHER, J. AND S. ROSIN.   1968.   Einfluss von Licht und Temperature auf die Schlupf-Aktivitat von *Chironomus nuditarsis* Str. Rev. Suisse Zool. 75:538-549.

KOSKINEN, R.   1968.   Seasonal and diel emergence of *Chironomus salinarius* Kieff. (Dipt., Chironomidae) near Bergen, Western Norway. Ann. Zool. Fenn. 5:65-70.

KURECK, A.   1966.   Schlupfrhythmus von *Diamesa artica* auf Spitsbergen. Oikos 17:276-277.

LEWIS, D. J.   1957.   Observations on Chironomidae at Khartoum. Bull. Entomol. Res. 48:155-184.

LINDEBERG, B.   1958.   A new trap for collecting emerging insects from small rockpools, with some examples of the results obtained. Ann. Entomol. Fenn. 24:186-191.

MILLER, R. B. 1941.   A contribution to the ecology of the Chironomidae of Costello Lake, Algonquin Park, Ontario. Univ. Toronto Stud., Biol. Ser. 49:1-63.

MORGAN, N. C.   1958.   Insect emergence from a small Scottish loch. Verh. Int. Verein. Theor. Angew. Limnol. 13:823-825.

_____ AND A. B. WADDELL.   1961.   Diurnal variation in the emergence of some aquatic insects. Trans. Royal Entomol. Soc. London 113:123-137.

MUNDIE, J. H.   1959.   The diurnal activity of the larger invertebrates at the surface of Lac La Ronge, Saskatchewan. Can. J. Zool. 37:945-956.

NEUMANN, D.   1971.   The temporal programming of development in the intertidal chironomid *Clunio marinus* (Diptera: Chironomidae). Can. Entomol. 103:315-318.

FIG. 9.   *Tanytarsus flavellus.* Diel periodicity of adult emergence from the littoral zone of Costello Lake, 19-20 August (A), and 11-12 September (B), 1965. Diel light distribution at the lake bottom is indicated by the horizontal bar; the lightly shaded areas indicate twilight periods. The time of sunset (EST) is indicated by a black arrow. Males are indicated by the black bars, females by the white bars.
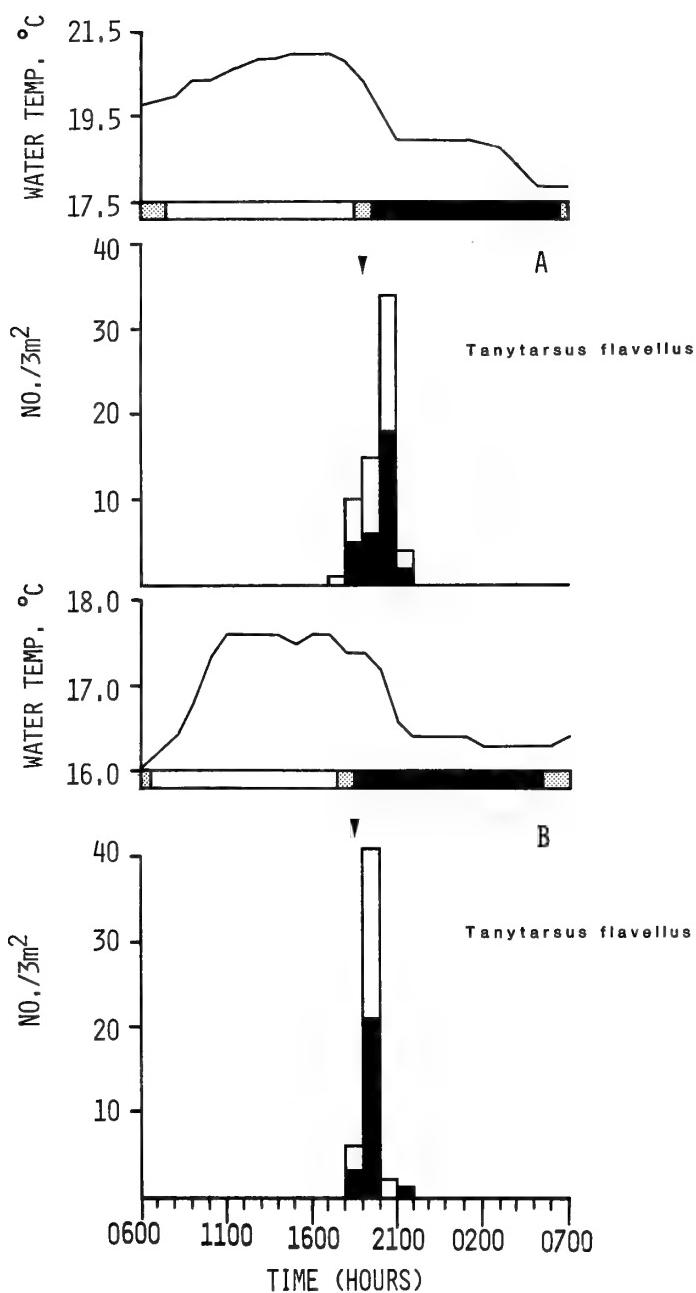
NIELSEN, E. T. 1962a. A note of the control of *Glyptotendipes paripes*. Mosq. News 22:114-115.

—————————. 1962b. Contributions to the ethology of *Glyptotendipes* (*Phytotendipes*) *paripes* Edwards. Oikos 13:48-75.

OLIVER, D. R. 1968. Adaptation of Arctic Chironomidae. Ann. Zool. Fenn. 5:111-118.

—————————. 1971. Life history of the Chironomidae. Ann. Rev. Entomol. 16:211-230.

PALMEN, E. 1955. Diel periodicity of pupal emergence in natural populations of some chironomids. Ann. Zool. Soc. Vanamo 17:1-30.

—————————. 1956a. Periodic emergence in some chironomids — an adaptation to nocturnalism. K. G. Wingstrand (ed.): Bertil Hanstrom, Zoological Papers in honour of his sixty-fifth birthday. pp. 148-256.

—————————. 1956a [1958]. Diel periodicity of pupal emergence in some North European chironomids. Proc. Int. Cong. Entomol., 10th. 2:219-224.

—————————. 1958. Periodic emergence in some North European chironomids. Verh. Int. Ver. Limnol. 41:817-822.

PHILLIPP, P. 1938. Experimentelle Studien zur Okologie von *Chironomus thummi* Kieffer. Zool. Anz. 122:237-245.

REMMERT, H. 1955a. Untersuchungen uber das tageszeitlich gebundene Schlupen von *Pseudosmittia arenaria* (Dipt., Chiron.). Z. vergl. Physiol. 37:338-354.

—————————. 1955b. Tageszeitlich gebundenes Schlupfen bein *Pseudsmittia arenaria* (Dipt. Chironomidae). Naturwiss. 42:261.

—————————. 1965. Uber den Tagesrhythmus arktischer Tiere. Zschr. Morphol. Okol. Tier. 55:142-160.

SCOTT, W., AND D. F. OPDYKE. 1941. The emergence of insects from Winona Lake. Invest. Ind. Lakes 2:3-14.

TOKUNAGA, M. 1932. Morphological and biological studies on a new marine chironomid fly, *Pontomyia pacifica*, from Japan. I. Morphology and Taxonomy. Mem. Coll. Agric. Kyoto Univ. 19:1-56.

—————————. 1934. Periodical emergence of a marine midge, *Pontomyia pacifica* Tokunaga. Proc. Kansai Entomol. Soc. 7.

WOOL, D. AND J. KUGLER. 1969. Circadian rhythm in chironomid species (Diptera) from the Hula nature preserve, Israel. Ann. Zool. Fenn. 6:94-97.

A Reconnaissance of the River Rhine using Chironomidae Pupal Exuviae (Insecta: Diptera)

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Abstract. — Samples of Chironomidae (Insecta: Diptera) pupal exuviae were taken from 62 stations along the River Rhine, its tributaries and associated lakes during a 3-week period in July/August 1981. Good samples proved easy to obtain by either hand-net or surface drift-net from all sections of the river, including both the alpine headwaters and the lowland reaches in Holland, as well as from the Bodensee and the Grand Canal d'Alsace.

The pattern of water quality was derived from consideration of both the sample diversity and the pollutional tolerance of taxa, and the results match well with the saprobien system classification (1969/74), and follow the main trends of chemical water quality.

The technique of exuvial sampling is shown to have a high potential as a tool for water quality assessment in large rivers of international importance.

Introduction

During the period of 23.7.81 to 10.8.81 the authors travelled the length of the Rhine from the Alps to the North Sea, taking a set of over seventy samples of chironomid pupal exuviae. Samples were taken from many of the more important tributaries and from the Bodensee as well as from the main river itself. Both surface drift-netting and bankside flotsam collecting techniques were employed, depending on the river conditions, although flotsam collections were preferred as they are less subject to diurnal variation (McGill, 1981).

There were two principal aims to this work. Firstly, to demonstrate that the technique of exuvial collecting could be carried out on a major international river, and secondly, to show whether the samples could be analysed to reveal the water qualities of the different sections of the river, as they have been successful in doing for rivers in Great Britain. Much of the British work has been carried out under contract with the Department of the Environment.

In the event, very little difficulty was experienced in obtaining large samples of exuviae from all the places sampled. In the Vorderrhein, Hinterrhein and Alpenrhein, the fast flow and turbulent nature of the river made it necessary to use the drift-nets extensively.

The exuvial types have been identified to genus, using keys prepared by the authors and Dr. P.H. Langton, and some species identifications have

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been checked by Dr. F. Reiss and Dr. P.H. Langton. A full species list will be published later.

The River Rhine — The Rhine is a major international river, flowing through Switzerland, Lichtenstein, Austria, France, West Germany and Holland. It has become famous not only for its navigational importance, but also for its pollutional state. Effluents from major industrial centres (such as Köln and the Ruhr Valley) as well as city sewage are carried in its waters, and are the cause of much concern to the downstream nations. Even the oligotrophic Bodensee (Lake Constance) is under threat from effluents originating in Switzerland.

The river (Figure 1) is 1320km long, and can conveniently be divided into sections for study. The VORDERRHEIN rises in Lake Toma on Piz Badus at 2344km above mean sea level, and links at Reichenau with the HINTER-RHIEN which flows from the Rheinwaldhorn glacier, to form the APLENRHEIN which then flows into the BODENSEE at 395m. Below the lake the river can be split into consecutive sections: the HOCHRHEIN from the Bodensee to just below Basel, the SUDLICHER and the NORDLICHER OBERRHEIN, from Basel to Karlsruhe and Karlsruhe to Mainz respectively, the MITTELRHEIN from below Mainz to just above Bonn, the NIEDERRHEIN from Bonn to Emmerich on the Dutch border, and finally the WAAL which flows from Emmerich to the North Sea (Friedrich & Müller, 1983). One of the exits has been dammed to form the HARINGVLIET, a freshwater lake, which has also been sampled in this study.

In general terms, serious pollution begins at Basel, which is the beginning of commercial navigation. From this point to just south of Karlsruhe the river forms the boundary between France and Germany and receives the saline effluents from French mines at and below Strasbourg. The river then flows past Mannheim where it is joined by the polluted river Neckar, past Worms and on to Mainz, where it receives another seriously polluted tributary, the Main. Throughout this Oberrhein section, the river has been subject to extensive restructuring to aid navigation, and cuts through sequences of old meanders which are more or less static. They form an important faunal refuge from which the main river can be continuously repopulated. Mention must also be made of the canal system near Strasbourg, and in particular the Grande Canal d'Alsace linking Basel and Strasbourg, and which carries most of the commercial shipping. It is regulated to maintain its flow at the expense of the main river, and during dry weather it may carry 90% of the total river flow (Rat von Sachverständigen für Umweltfragen, 1976).
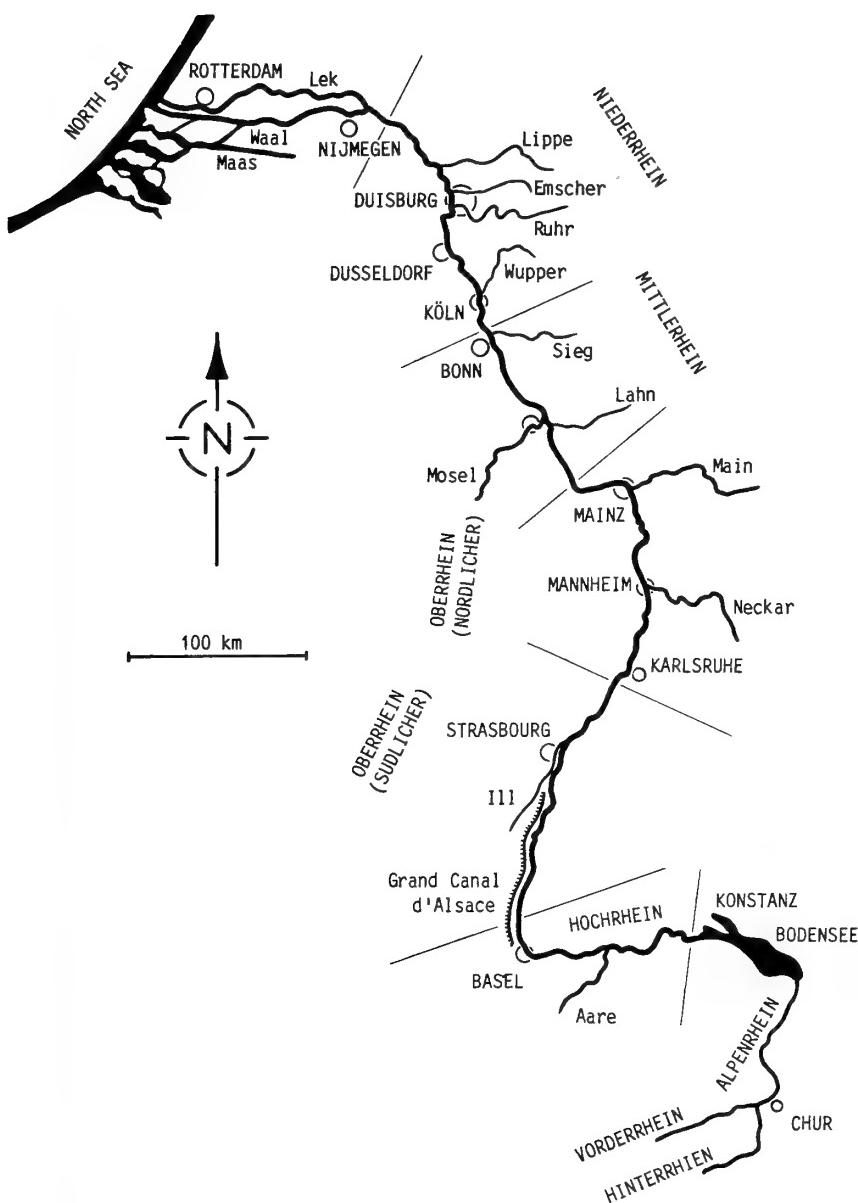
FIG. 1. Sketch map of the River Rhine showing some of the principal cities and tributaries, and the regional divisions.

At Mainz the waters of the Main flow along the north bank, and are kept largely separate from the Rhine water by the presence of midstream islands until they mix completely at Bingen where the river enters the Mittelrhein gorge. The water here is very deep and fast flowing, with steep rocky banks. It is joined by the Mosel at Koblenz, and then flows on to Bonn, where it emerges from the gorge into a more open countryside. From here it may be termed the Niederrhein, and is subject to the most severe pollution of its whole course, from sewage and industrial effluents from Bonn, Leverkusen, Köln, Dusseldorf and the great industrial complex of the Ruhr. The highly polluted tributaries of the Wupper, the Ruhr, the Emscher and the Lippe which enter in this section, were selected for special study, as it was considered that they would show the characteristics of extreme pollution.

Below Emmerich the Rhine enters Holland, and divides at Nijmegen into two rivers, the Lek and the Waal. Of these two, the Waal is the more important, but there are many connecting channels and canals both between them and with the Maas. This network of waterways links Rotterdam and the Hook of Holland, as well as cities further afield. The Lek passes through Rotterdam, and together with the Waal and Maas discharge to the North Sea at the Hook of Holland.

Many of the features of the Rhine have been manipulated by man in order to maintain navigation. The banks in many areas of the lower river have been stabilised with groins set out at right-angles to the bank. These form pockets of relatively still water, but even so the passage of the great barges cause considerable wave action on the shore. Further up the river, especially in the Mittelrhein, the channel is divided by a series of islands. In order to maintain an adequate channel for shipping under dry weather conditions, walls associated with the islands have also been constructed in the river, for instance at Mainz. These are only visible above water at low water, but provide lentic areas where sediment may be deposited, in the centre of the fast-flowing main stream. In general, however, the river may be considered as a turbulent and rapid river throughout most of its course, with a bed principally of stones and gravel. Large accumulations of sand and silt can only occur at the downstream end, especially in the delta and estuary regions.

METHODS

Sampling and sampling stations — Table 1 gives a list of the stations from which samples were taken during this survey. They were selected to give a complete coverage of the river, and included samples from the lower end of

TABLE 1. List of sampling sites.

VORDERRHEIN
  VR1   Oberalppass
  VR2   Disentis Bridge
  VR3   Tavanasa Bridge

HINTERRHEIN
  HR1   Hinterrhein
  HR2   Clugin Bridge
  HR3   Rodels Bridge

ALPENRHEIN
  SR1   Untervaz Bridge
  SR2   Sevelin Bridge
  SR3   Diepoldsau Bridge
  SR4   Altenrhein Zoll

BODENSEE
  B1   Aeschach
  B2   Nonnenhorn
  B3   Horn
  B4   Berlingen (Untersee)

HOCHRHEIN
  R1   Rheinklingen
  R2   Eglisau
  R3a   Murg (Laufenburg)
  R3b   Murg
  R4   Rheinweiler

OBERRHEIN (SUDLICHER)
  R5   Weisweil
  R6   Ichenheim
  R7   Sollingen

OBERRHEIN (NORDLICHER)
  R8   Leopoldshafen
  R9   Germersheim
  R10   Philippsburg
  R11   Rheinhausen
  R12   Speyer
  R13   Bruhl
  R14   Rheindurkheim
  R15   Mainz, Mombacher (S. bank)
  R16   Mainz, Biebrich (N. bank)
  R17   Assmannshausen

MITTELRHEIN
  R18   Loreley
  R19   Irlich
  R20   Erpel (Remagen Bridge)

NIEDERRHEIN
  R21   Niederkassel
  R22   Leverkusen
  R23   Hitdorf
  R24   Kaiserwerth
  R25   Gotterswickershamm East
  R26   Gotterswickershamm
  R27   Rees
  R28   Emmerich

WAAL
  W1   Dodewaard
  W2   Rossum
  W3   Brakel

HARINGVLIET
  H1   Hellevoetsluis

Tributaries

AARE
  AA1   Dottingen

GRAND CANAL D'ALSACE
  CA1   Chalampé
  CA2   Geiswasser

NECKAR
  NE1   Neckarhausen

MAIN
  MA1   Russelsheim (10 samples)

MOSEL
  MO1   Lay (10 samples)

WUPPER
  WU1   Vohwinkel
  WU2   Mungsteiner Brucke
  WU3   Landwehr
  WU4   Burrig (Leverkusen)

RUHR
  RH1   Duisburg Hafen

EMSCHER
  RE1   Stapp

LIPPE
  LI1   Oberlippedorf

some of the major tributaries. Help in the selection was given by Professor Kinzelbach of Mainz University, and Dr. Caspers of Bonn University, and is here gratefully acknowledged.

At each station, shoreline flotsam collections were made with a fine-meshed hand net on a triple extendable handle, or with a series of 3 surface drift-nets, 2 with openings of 10 x 30 cm and one of 10.5 x 61 cm. The net mesh was 250 μm aperture in each case. Each sample was briefly examined in a white bowl to confirm that an adequate number of exuviae had been taken, before moving on to the next station. All samples were sieved at the water's edge through a 250 μm sieve, placed in polythene bags, labelled, and fixed with formalin. They were then placed in a sealed, insulated container for transportation.

Measurements were made at each station of the water temperature, conductivity, pH and Dissolved Oxygen, using HACH portable meters, Models 17250, 19000 and 16046. The values must be treated with caution, however, since they were necessarily taken from the shoreline, and may bear little resemblance to measurements taken in the main stream. The turbidity was also recorded by passing 20 ml of water through a 13 mm diameter glass fibre filter paper, which was then mounted on the record card. It could be seen that the wash from a passing barge significantly increased the turbidity, but that the silt then settled rapidly again.

Laboratory procedure and sample analysis — Each sample when opened was rinsed through a 250 mu sieve to remove the formalin, and suspended in a bowl of water. Subsamples were taken by the ''scoop'' method (Wilson & McGill, 1977, 1979) and approximately 200 exuviae were mounted on slides, 20 to a slide, using dimethyl-hydantoin-formaldehyde mountant.

These exuviae were identified, and counted, and the results stored on disc using a Commodore 3032 Series PET Computer. The samples from each river section were added to give ''amalgamated samples,'' which reflect the general characteristics of the section in question. These, together with the original samples were then analysed to reveal the percentage composition of species and subfamilies, and the Menhinick and Shannon-Weaver Diversities (see Hellawell, 1978).

The assessment of water quality followed the technique developed under contract with the Department of the Environment for the River Trent and other British rivers (Wilson, unpub. reports to the DOE, 1976-82) which entailed the allocation of each species or taxon of chironomid identified to four categories based on an empirical knowledge of their pollution ''tolerance'' (Wilson and McGill, 1982). The tolerance considered was principally with respect to low oxygen and organic pollution. Category A was

the least tolerant, B and C intermediate, and D the most tolerant. Each of these was calculated both for species presence/absence data and for relative abundance data.

RESULTS

In this paper the samples taken down the main river have been amalgamated for each region (see Figure 1 and Table 1). Samples taken on tributaries have been given individually: in most cases only a single sample was taken near the point of discharge of the tributary to the main river, but two stations were sampled on the Grand Canal d'Alsace, and four on the Wupper.

Table 2 gives some of the more important data derived from the samples, including the percentage of taxa and exuviae in the tolerance categories A, B, C and D, the Menhinick and the Shannon-Weaver diversities, as well as the percentage of sediment-dwellers. It appears from current work on the River Trent in Britain, that the sediment-dwellers may be more exposed to the effects of industrial and heavy metal pollution, and may be selectively eliminated where this occurs. Certainly the levels of heavy metals in the Rhine sediments are very high, especially at the lower end of the river (Förstner and Wittmann, 1979; Müller, 1971; van der Veen and Huizenga, 1980).

Taxa have been allocated to tolerance categories and as sediment-dwellers according to the authors' best estimates, after a close study of the literature, coupled to personal observations and subsequently modified by discussion with colleagues. As more detailed information becomes available on the ecology of the different species, this categorization will undoubtedly have to be modified. The categories chosen are as follows:

A. INTOLERANT: found only in clean waters.
B. FACULTATIVE/INTOLERANT: common in clean waters, but occasionally found in situations of mild pollution.
C. FACULTATIVE/TOLERANT: often found in abundance in mildly polluted waters, but also present in clean waters.
D. TOLERANT: capable of survival under conditions of severe pollution, but may also be found in low numbers in clean waters.

Of the two diversity indices used, the Menhinick diversity depends on the numbers of taxa relative to the numbers of exuviae sampled, whereas the

TABLE 2.   Basic sample data for the principal regions of the River Rhine and selected tributaries.

	No. of samples	No. of taxa	No. of exuviae	Diversity		Quality Categories (%)								Sediment dwellers (%)	
				Men-hinick D	Shannon Weaver H	Taxa +/−				Rel. Abund.					
						A	B	C	D	A	B	C	D	taxa	exuviae
VORDERRHEIN	3	36	620	1.45	2.59	45	22	19	14	58	12	28	2	8.3	3.1
HINTERRHEIN	3	35	589	1.44	2.85	40	29	20	11	63	12	17	8	17.1	5.1
ALPENRHEIN	3	49	567	2.06	2.80	37	27	18	18	64	13	12	11	14.3	3.7
BODENSEE	4	57	876	1.93	3.21	14	30	19	37	10	24	21	45	68.4	42.1
HOCHRHEIN	5	63	1040	1.95	3.36	25	30	18	27	30	33	20	17	44.4	34.5
OBERRHEIN (S)	3	35	595	1.43	2.27	14	35	20	31	3	40	22	35	28.6	3.4
OBERRHEIN (N)	10	50	2142	1.08	2.67	18	28	20	34	14	22	42	22	36.0	2.5
MITTELRHEIN	3	28	667	1.08	2.27	21	22	21	36	10	43	38	9	21.4	2.4
NIEDERRHEIN	8	27	1787	0.64	1.63	15	22	22	41	1	37	48	14	18.5	0.7
WAAL	3	19	668	0.74	2.12	10	32	16	42	1	19	31	49	13.6	6.0
HARINGVLIET	1	12	220	0.81	1.76	8	17	17	58	40	14	27	19	58.3	84.6

Tributaries

AARE														
Dottingen	1	35	214	2.39	2.69	29	24	14	23	52	29	3	16	45.7	33.6
GRAND CANAL D'ALSACE														
Chalampé	1	16	204	1.12	2.09	19	19	31	31	11	36	38	15	12.5	1.5
Geiswasser	1	20	222	1.34	1.70	20	30	25	25	7	64	15	14	15.0	1.8
NECKAR														
Neckarhausen	1	17	210	1.15	1.85	0	24	24	52	0	8	33	59	29.4	5.1
MAIN														
Russelheim	1	15	214	1.03	1.69	0	20	27	53	0	2	18	80	26.7	3.7
MOSEL														
Lay	1	19	240	1.23	1.73	11	32	26	31	1	17	47	35	21.1	7.1
WUPPER														
Vohwinkel	1	20	228	1.32	2.36	25	15	20	40	10	9	35	46	10.0	5.3
Mungsteiner	1	22	200	1.56	2.01	18	9	27	45	4	5	53	38	18.2	11.0
Landwehr	1	3	109	0.22	0.07	0	0	67	33	0	0	1	99	3.33	98.9
Burrig	1	4	239	0.26	0.08	0	0	50	50	0	0	1	99	25.0	98.7
RUHR														
Duisburg	1	23	204	1.61	2.31	4	22	26	48	3	11	25	61	43.5	26.5
EMSCHER														
Stapp	1	3	204	0.21	0.06	0	33	33	33	0	1	1	98	33.3	99.0
LIPPE														
Oberlippedorf	1	18	217	1.22	1.51	0	28	22	50	0	5	81	14	16.7	2.3

Shannon-Weaver diversity is calculated from the relative abundance of the different taxa. The formulae are as follows: —

Menhinick Diversity = $\dfrac{S}{N^{0.5}}$

(where S = total taxa, and N = total exuviae)

Shannon-Weaver Diversity = - Sigma $Pi.\log_{10}Pi$

(where Pi is the proportion of individuals in the ith taxon).

Bar-charts giving the relative percentages of subfamilies and tribes are shown in Figure 2 for the main Rhine regions and in Figure 3 for the tributaries. Table 3 shows how the numbers of species in the principal sub-families and tribes found in the Rhine alter between the regions. The numbers of species given in the table are estimates of those that would be expected to occur in samples of 500 exuviae in each case.

The actual sample size for the different regions varies from 220 to 2142 exuviae, depending on the number of samples amalgamated, and the estimated species count was calculated by assuming that the Menhinick diversity remains constant for different sized samples (a condition that is fulfilled within a 10% to 15% error, see Wilson, unpub. report to the DOE, 1980), and then working out the number of species that would give the same diversity in a sample of 500 exuviae. This procedure therefore does not give the maximum number of species which could be found, but facilitates comparisons between the regions.

The Vorderrhein, Hinterrhein and Alpenrhein are dominated by Orthocladiinae (with estimates of 24, 24 and 38 spp. respectively), each section has only a single Chironomini and 4 or 5 Tanytarsini; Bodensee is dominated by Chironomini (17 spp.) and Tanytarsini (11 spp.), and has a reduced number of Orthocladiinae (8 spp.); the Hochrhein again shows Orthocladiinae as dominant (19 spp.), but with a significant number of Chironomini (12 spp.) and Tanytarsini (6 spp.); while the remainder of the river shows a falling-off in numbers of species reaching the lowest point in the Niederrhein with only 7 Orthocladiinae, 4 Chironomini and 2 Tanytarsini. It is interesting to contrast Bodensee with the Haringvliet, which have totals of 43 and 18 species respectively.

In Figures 4 and 5 the proportions of taxa and exuviae are plotted as proportions of the appropriate diversity index. Taxa presence/absence data are

FIG. 2.   Bar-charts of percentage relative abundance of taxa, and the Menhinick Diversity, for amalgamated data for the different region of the River Rhine. (Key: Tanypodinae (ex. Pentaneurini), black; Pentaneurini, cross-hatched; Diamesinae, stippled; Prodiamesinae, squares; Orthocladiinae, white; Chironomini, vertical hatching; Tanytarsini, dots).
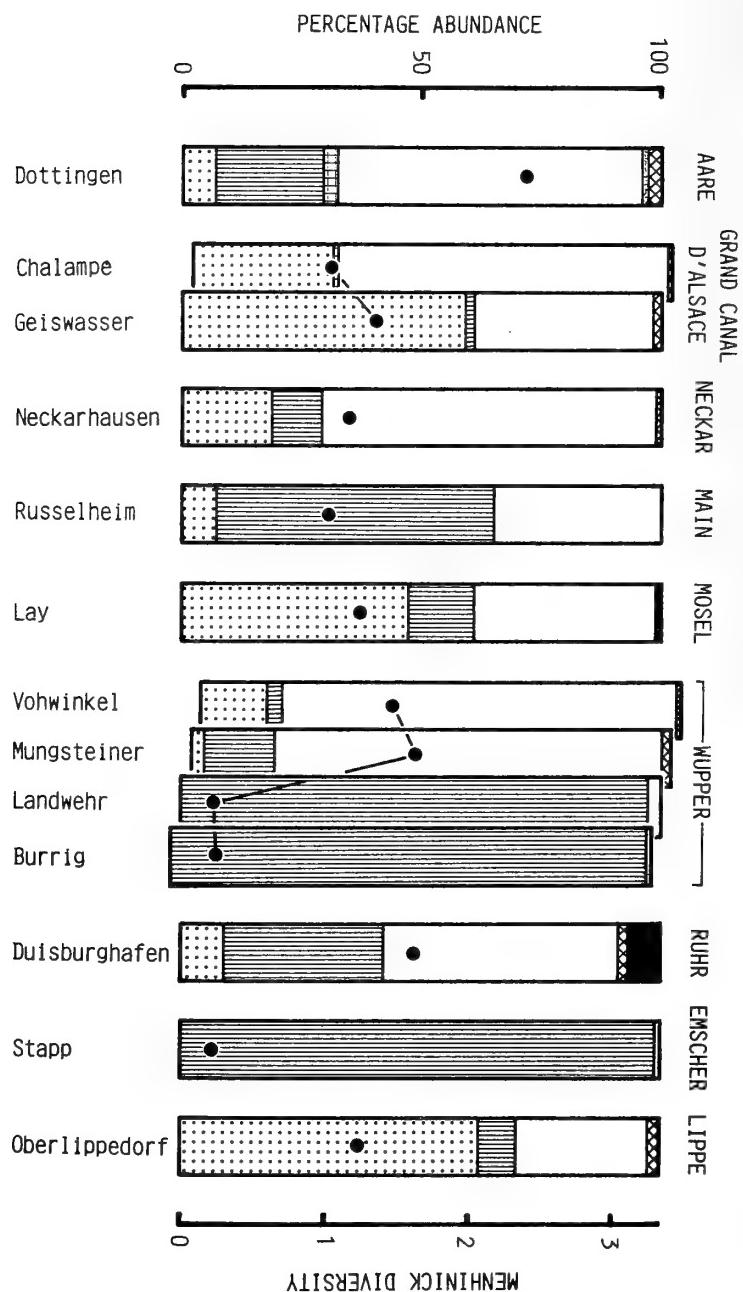
associated with the Menhinick diversity, and the relative abundance data with the Shannon-Weaver diversity.

The diagrams in Figures 4 and 5 give a visual indication of water quality as they combine the diversity with the pollutional tolerance categories (A to D). The authors feel that it is very important to consider both diversity and tolerance in arriving at an assessment of water quality. High diversity coupled to a high proportion of intolerant taxa indicates a river of excellent quality, if they are both low, then the water is strongly polluted. If the diversity is low, but the proportion of intolerants high, then the water is of good quality, but the fauna is "restricted" through natural physical or chemical conditions. This condition is typical of high mountain areas with low productivity, but no pollution. If the diversity is high and coupled to a high proportion of tolerant forms, then the water is organically "enriched", but not severely polluted. Other categories may be devised, depending on the setting of limiting values for the diversity and proportion of intolerant/tolerant taxa, and the limiting values used in this study are given in Table 4.

Lakes normally have a high proportion of sediment-dwellers, and as these tend to be more tolerant, they may be assigned to a lower category than is warranted; care therefore must be taken in the interpretation of the data. The joining of the points in these diagrams by straight lines is not intended to imply a gradation of intermediate values, but only to facilitate the eye in comprehending the overall patterns.

The term "sediment-dwellers" as used in this study, is defined as those larvae which normally live in sand, silt or mud; but excludes those species whose larvae are principally associated with only sparsely silted rocks.

It is important to distinguish between the data based on the presence/absence of taxa, and that based on the relative abundance of exuviae, and the two data sets give different information on the river conditions. Presence/absence of species gives equal weighting to each species present, however low their numbers, and can therefore be significantly biased by the occurrence of rare species. On the other hand, each species of chironomid has its own period (s) of maximum emergence, and so the actual numbers of exuviae collected may vary significantly between different seasons of the year. Thus single samples taken at different seasons will not give the same relative abundances, and should not strictly be compared.

FIG. 3. Bar-charts of percentage relative abundance of taxa, and the Menhinick Diversity, for data from selected tributaries of the River Rhine. (Key: Tanypodinae (ex. Pentaneurini), black; Pentaneurini, cross-hatched; Diamesinae, stippled; Prodiamesinae, squares; Orthocladiinae, white; Chironomini, vertical hatching; Tanytarsini, dots).

TABLE 3. Number of chironomid species in the main subfamilies and tribes found in the principal sections of the River Rhine. The numbers are referable to a sample of 500 exuviae in each case by proportioning according to the Menhinick diversity (for further details see text). Total species and exuviae for each section are also given.

Subfamilies & Tribes	Vorder rhein	Hinter rhein	Alpen rhein	Boden see	Hoch rhein	Ober rhein Sud	Ober rhein Nord	Mittel rhein	Nieder rhein	Waal	Haring vliet
Tanypodinae (ex. Pentaneurini)	0	1	1	5	4	2	2	0	0	1	2
Pentaneurini	1	0	0	1	2	1	1	2	2	1	0
Diamesinae	3	2	1	1	1	0	0	0	0	0	0
Prodiamesinae	0	0	1	0	1	0	0	0	0	0	0
Prodiamesinae	24	24	38	8	19	13	10	12	7	6	6
Orthocladiinae	1	1	1	17	12	11	9	8	4	7	6
Chironomini	4	5	5	11	6	6	3	3	2	2	5
Tanytarsini											
TOTALS	32	32	46	43	44	32	24	24	14	16	18
Total species actually found	36	35	49	57	63	35	50	28	27	19	12
Total exuviae examined	620	589	567	876	1040	595	2142	667	1787	668	220
Menhinick diversity	1.45	1.44	2.06	1.93	1.95	1.43	1.08	1.08	0.64	0.74	0.81

Single samples comprising a set taken all within a short priod of time, as were those from the Rhine, may have their relative abundances compared within the set, but should not be compared with data from other seasons or places. Relative abundance data becomes more valid when a series of samples has been taken from each station at different seasons, for instance monthly through the year.

The presence/absence data is not so subject to these restrictions, as most of the river species have extended emergence periods during which they can be taken in a sample, but perhaps only at a low level of abundance. Experience has shown that presence/absence data give more consistent results between different seasons than do relative abundance data (Wilson, unpub. reports to the DOE, 1976-82). More weight is therefore placed on presence/absence data in this present study.

In addition, different interpretations must be applied to the two data sets. The presence of a species implies that it has the ability to survive in the habitat, and that its niche is supported by the prevailing conditions. The community of species therefore outlines the range of niches available and hence the range of conditions within the river. By considering the community as a whole, one may to a large extent avoid the problems of using indicator species which may be present or absent for a number of unrelated reasons. It also avoids undue emphasis being placed on any single exuviae which may be present by chance. All the species in the community are linked together by the actual water quality in which they all live, and which sets the limits of the extremes of tolerance within which the community exists.

Within these limits, various other factors, such as substrate, food, predation etc. all play their parts in shaping the community, but they will often exert more control on the numbers of each species present than on its absolute survival. Relative abundance data can give a measurement of the success of different species, and therefore indicate the relative extent of each niche within the ecosystem. It is an oversimplification to state that the numbers of a species indicate the amount of substratum available to it and therefore that a high proportion of mud-dwellers indicates a high proportion of mud in the substratum, but in general this must be true, and can be usefully examined in assessing river conditions from exuvial samples.

To categorize the samples with respect to water quality, both the diversity and the proportions of categories A, B, C and D must be taken into account. Table 5 gives pollutional categories allocated according to the scheme shown in Table 4, which can be compared with the saprobic data for 1969-74 (Rat von Sachverständigen für Umweltgragen, 1976). Only presence/absence data has been used to calculate the values for Table 5.

TABLE 4. Table showing the method of deriving the water quality classification from exuvial data, and their relationship to the saprobien system.

Water Quality Classification

Quality Class	Menhinick Diversity	$\dfrac{(A+B)}{(A+B+C+D)}$ x100%	Comments	Saprobien System
1A	High Low	High High	excellent good (restricted)	Ia oligosaprobic
1B	High Medium	Medium High	good (+/− enriched) good	Ib o-B-meso
2	High Medium	Low Medium	doubtful (enriched) doubtful	II B-meso
3	Medium Low	Low Medium	poor poor	III a-meso
4	Low	Low	badly polluted	IV polysaprobic

Table of quality limiting values

	Menhinick Diversity	$\dfrac{(A+B)}{(A+B+C+D)}$ x100%
High	= >1.3	= >65%
Medium	0.6-1.29	31-64%
Low*	= <0.59	= <30

(*If the diversity = <0.3 and %(A+B)<60% then Class 4)
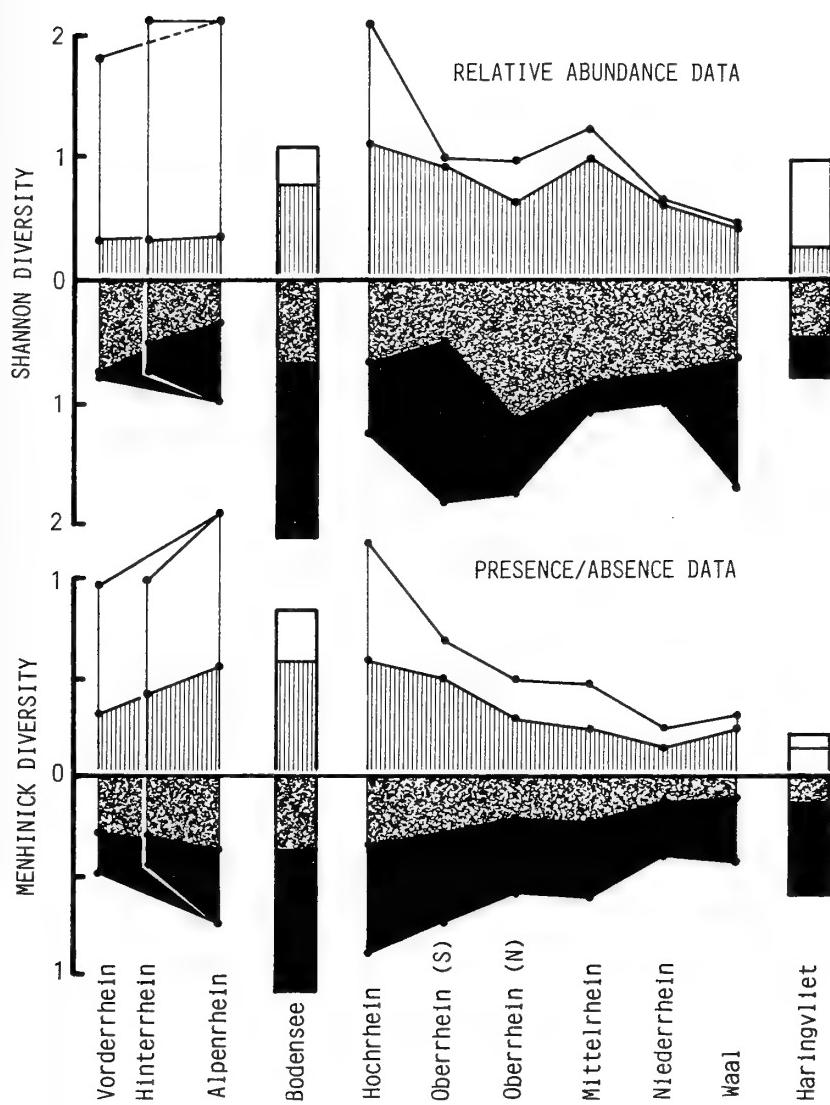
Fig. 4. Water quality diagrams for the principal regions of the River Rhine, with the tolerance categories A, B, C & D plotted as proportions of the diversity. Upper diagram: relative abundance data and Shannon-Weaver Diversity; lower diagram: taxa presence/absence data and Menhinick Diversity. (Key: A, white; B, vertical hatching; C, stippled; D, black).

DISCUSSION

Of the two major objectives, that of testing the sampling procedure on a major international river, has been satisfactorily accomplished. Good samples of exuviae were readily taken at each sampling station. The wide applicability of the technique has therefore been clearly demonstrated. No other single sampling technique can obtain comparable samples from rapid, stony, mountain rivers, from large, deep, lowland rivers, as well as from canals and lakes.

The second objective, of analysing the samples to reveal the water quality, has also been satisfactorily achieved using techniques developed for British rivers. It is difficult to prove that the results are in accord with the currently known physics and chemistry of the Rhine, since the information available to the authors is mostly sketchy or out of date. For the purpose of this preliminary reconnaissance, however, it is sufficient to confirm that the exuvial samples and analyses reflect the major trends in the quality of the Rhine. Table 5 shows that the saprobity assessments of 1969-74 match well with the quality classifications derived from the exuvial data, with if anything, some recent improvements being demonstrated. There is evidence that levels of organic and heavy metal pollution (but not salt or organo-chlorides) have decreased between 1971 and 1980, especially in the Nieder-rhein (Arbeitsgemeinschaft Rhein-Wasserwerke, 1981; Müller, 1979; Son-theimer, Gimbel and Weindel, 1979).

Figure 4 illustrates the good quality of the Vorderrhein and Hinterrhein which have an excellent, if a little restricted, chironomid fauna. The Alpenrhein has a highly diverse fauna again of good quality, but demonstrating enrichment in this fast-flowing section of the river.

The Bodensee has a rich chironomid fauna (Reiss, 1968), and the current samples show that there is a high proportion of more tolerant forms. There is also a high proportion of sediment-dwellers — a feature to be expected in a lake. It therefore appears that the water quality is not first-class, being assessed at Class 1B. However, care must be exercised in the interpretation of lake samples as no detailed work has yet been done to show the relationships between the shore line exuvial collections and the trophic status. It is likely that lakes will have to be assessed against a modified set of quality criteria.

The Hochrhein has a good fauna, and is tentatively classed as IB along with its major tributary the Aare. The Aare has an exceptionally high diversity, which probably indicates slight enrichment. Work by Bloesch (1977), Caspers (1980) and Kinzelbach (1978) demonstrate the good diversity of the general invertebrate fauna in this region.

TABLE 5. Comparison between saprobic classification and exuvial classification for the principal regions of the Rhine and selected tributaries.

Region	Quality classification	
	Saprobic (1969-74)	Exuvial (1981)
River Rhine		
Vorderrhein	?	1A
Hinterrhein	?	1A
Alpenrhein	IIa	1B
Bodensee	?	1B
Hochrhein	IIa	1B
Oberrhein (S)	IIa	1B
Oberrhein (N)	IIIa	2
Mittelrhein	IIIa	2
Niederrhein	IIIa	2 (low)
Waal	IIb	2
Haringvliet	?	3
Tributaries (in rank order)		
Aare (Dottingen)	IIb	1B
Gd. Canal d'Alsace (Geiswasser)	?	1B
Wupper (Vohwinkel)	IIIb	1B
Gd. Canal d'Alsace (Chalampé)	?	2
Mosel (Lay)	IIa	2
Wupper (Mungsteiner Br.)	IV	2 (enriched)
Ruhr (Duisburghafen)	IIa	2 (enriched)
Neckar (Neckarhausen)	IIIB	3
Main (Russelheim)	IIIb	3
Lippe (Oberlippedorf)	IIIb	3
Wupper (Landwehr)	IV	4
Wupper (Burrig)	IV	4
Emscher (Stapp)	IV	4

The Oberrhein shows a progressive fall-off in quality downstream. Although the Südlicher Oberrhein is still classed as IB, it suffers a reduction in diversity and in % Intolerant, compared with the Hochrhein (Figure 6). The percentage of sediment-dwellers also falls off very rapidly at this point. The Südlicher Oberrhein receives a large quantity of effluent from industry and sewage below Basel and Strasbourg.

Samples were also taken from the Grand Canal d'Alsace which runs parallel to this section of the Rhine. It is a very large concrete channel which carries most of the commercial traffic between two cities. Exuviae were found in abundance along the concrete canal edge, and the analyses show that the fauna was Class 2 at Chalampé but improved downstream to Class IB at Geiswasser.

The Nordlicher Oberrhein shows a further reduction in diversity. It receives the waters of the Neckar and the Main, both of which show a polluted chironomid fauna exemplified by a severe reduction of the intolerant categories A and B. The Neckar fauna is more restricted than that of the Main, and may be subject to more severe industrial, as opposed to organic, pollution than the Main.

It was established by taking samples from both sides of the river at Mainz and looking at the species composition, that the Main affects only the north bank of the Rhine downstream of its entry. The waters of the Main and the Rhine mix completely only at Bingen, where the river enters the narrow Mittelrhien gorge (Kinzelbach, pers. comm.).

In the Mittelrhein the river is steep-sided and rocky, and is therefore different in character from the sections above and below. The quality index does not change, however, nor does the taxa composition alter to any great extent, but an improvement can be seen in an increase of the relative abundance of category A and B exuviae. There is also a reduction in the % sediment-dwelling taxa. The Mosel is the principal tributary entering in this section, but has a higher exuvial quality index (Class 2) than the Neckar or Main (both Class 3).

The Neiderrhein flows through the industrial heart of Germany and receives the drainage from some of the most highly populated and industrial areas in the country. It is not surprising therefore that there is both a reduction of diversity and of intolerant taxa and exuviae in this section, although on the quality assessment it is still just in Class 2.

Of the tributaries sampled, the lower stations of the Wupper and the Emscher reveal a most seriously polluted condition. The set of samples taken down the Wupper show how this river alters under the impact of heavy sewage pollution. The top station at Vohwinkel lies above the major sewage works; Mungsteiner Brucke is characterised by a great increase of
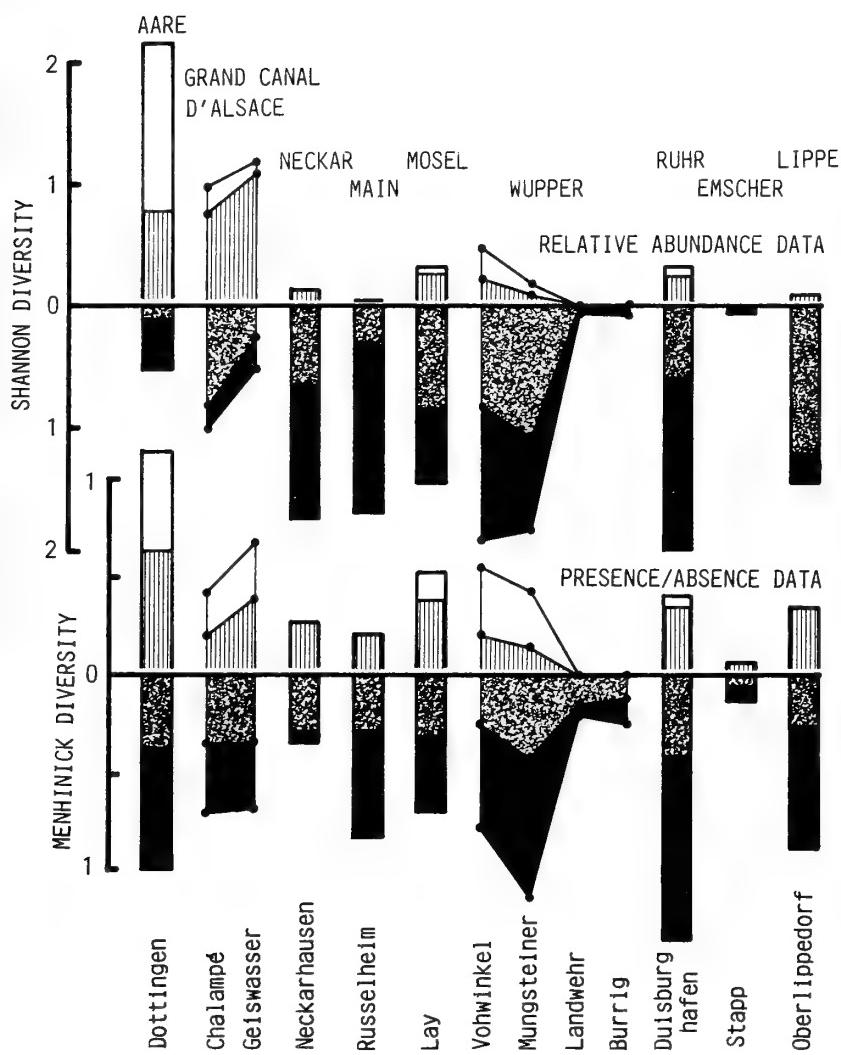
FIG. 5. Water quality diagrams for selected tributaries of the River Rhine, with the tolerance categories A, B, C & D plotted as proportions of the diversity. Upper diagram: relative abundance data and Shannon-Weaver Diversity; lower diagram: taxa presence/absence data and Menhinick Diversity. (Key: A, white; B, vertical hatching; C, stippled; D, black).

tolerant taxa and reduction of intolerant taxa; while at Landwehr the sample contained tolerant taxa only, coupled to an exceptionally low diversity, indicating very severe pollution. This condition persists downstream to Burrig, just above the confluence with the Rhine. The Emscher appeared to be a fast-flowing canalised river with clear water of very high conductivity (4000 μuS), which foamed excessively over a weir at its point of discharge to the Rhine. At each of these very highly polluted stations the chironomid population was reduced almost completely to a single species, *Chironomus riparius* Meigen.

In contrast, the Ruhr was revealed as an organically enriched river of Class 2, with a diverse, but tolerant, fauna. The Lippe was assigned to Class 3 and appeared to be rather more polluted.

There is no significant change in the condition of the Rhine as it passes into Holland. Figure 4 shows that there is only a marginal increase in the taxa diversity in the Waal as compared with the Niederrhein. The relative abundance data, however, show an increase in the proportion of tolerant exuviae, perhaps due to enrichment with organic matter.

In the Waal the percentage of sediment-dwelling species (as previously defined) drops to the lowest value for the whole river below Bodensee, although their relative numbers increase slightly. It is possible that the sediment, in which the heavy metals tend to accumulate (Müller, 1979), is too toxic to maintain a good chironomid fauna.

In the single Haringvliet sample distinct changes in the fauna can be observed, probably consequent on its being in effect a freshwater lake. These changes include an increase in taxa diversity, and in category D taxa. This is balanced by an increase in the proportion of intolerant exuviae. In no way, however, does it approach the good quality of the Bodensee, and has been allocated to Class 3 using the existing quality criteria; but it must be pointed out again that this assessment may be too low a value for lentic situations.

Of the actual genera and species identified, a few require detailed mention. *Chironomus riparius* is a well-known indicator of organic enrichment, and made up over 95% of the exuvial samples from the Emscher and the lower Wupper. This species was also found in the Rhine itself at Gotterswickershamm below the Emscher inflow; and elsewhere was present low numbers in the Waal, the Main and the Hochrhein.

There were two species of *Rheotanytarsus* exuviae present throughout most of the system, *R. photophilus* (Goetghebuer) and *R. rhenanus* Klink. The latter has been recently identified by Klink (in press). They dominated the fauna of the Mittelrhein and Niederrhein where the larval tubes could be seen very commonly on rocks along the shoreline. High numbers of *Rheotanytarsus* have previously been reported near Bonn by Caspers
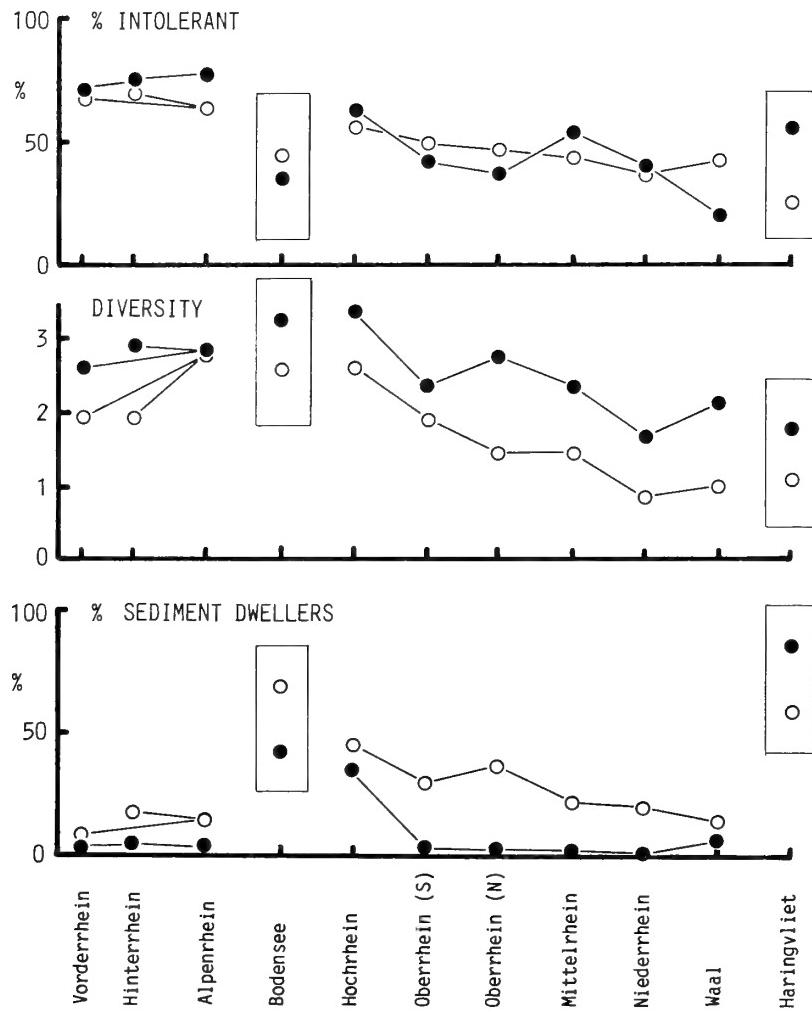
FIG. 6. Graphs of % Intolerant (open circles, taxa; closed circles, relative abundance), Diversity (open circles, Menhinick; closed circles, Shannon-Weaver) and % Sediment-dwellers (open circles, taxa; closed circles, relative abundance) for the principal sections of the River Rhine.

(1980b). They were also present commonly in the Südlicher Oberrhein above Strasbourg, and in the Grand Canal d'Alsace. Below Strasbourg in the Nordlicher Oberrhein, their numbers were remarkably low, as they were also in the Neckar and Main. High numbers were found in the Mosel, the Lippe and on the south bank of the river at Mainz, opposite to the point of inflow of the Main.

The larvae of *Rheotanytarsus* are filterfeeders, and therefore depend on the suspended organic matter including phytoplankton which is commonly present (Backhaus & Kemball, 1978) and their distribution must be related to the balance between the availability of particulate food and the avoidance of areas of heavy siltation. Field observations showed that the suspended matter in the river increased markedly downstream, building up after the entry of the Main to a maximum in the Niederrhein and Waal. This distribution coincides with the dominance of *Rheotanytarsus,* and it may be that the fast flow or the frequent wave action on the shore due to passing barges is sufficient to keep the larvae free from excess silt deposition. An interesting difference in the distribution of the two species was noted, with *R. photophilus* dominating the more highly polluted regions and tributaries in the lower part of the river, and *R. rhenanus* more common in the Hochrhein.

More detailed descriptions of the distributions of particular species or genera could be made, some of which appear to be linked to water quality, but are omitted because much would be speculative. It is clear, however, that sampling chironomid pupal exuviae has great potential as a simple and cheap technique in the biological assessment of water quality. It is applicable to both lotic and lentic waters, although it may find particular application under conditions where other forms of sampling are difficult or dangerous. The authors feel that it may also prove of use in detailed monitoring of rivers of international importance.

REFERENCES

BACKHAUS, D. AND A. KEMBALL. 1978. Gewässergütverhältnisse und Phytoplanktonentwicklung im Hochrhein, Obberhein und Neckar. Arch. Hydrobiol. 82:166-206.

BLOETSCH, J. 1977. Bodenfaunistische Untersuchungen in Aare und Rhein. Schweiz. Z. Hydrol. 39:46-67.

CASPERS, N. 1980a. Die Makrozoobenthos-Gesellschaften des Hochrheins bei Bad Säckingen. Beitr.naturk.Forsch.SüdwDtl. 39:115-142.

_____. 1980b. Die Makrozoobenthos-Gesellschaften des Rheins bei Bonn. Decheniana (Bonn) 133:93-106.

FRIEDRICH, G. AND D. MULLER. 1983. Rhine. In: WHITTON B.A. (Ed.) Ecology of European Rivers. Blackwell, Oxford.

HELLAWELL, J.M. 1978. Biological surveillance of rivers. N.E.R.C. Handbook, Water Research Centre, Stevenage.

KINZELBACH, R. 1978. Veränderungen der Fauna des Oberrheins. Beih. Veröff. Naturschutz Landschaftspflege Bad.Württ. 11:291-301.

KLINK, A. in press. *Rheotanytarsus rhenanus* n.sp., a common midge of the lithorheophilic fauna in large lowland rivers (Diptera, Chironomidae). Ent. Bei., Amsterdam.

McGILL, J.D. 1981. Distribution of Chironomidae (Diptera) throughout the River Chew drainage system, Avon, England. Unpublished PhD thesis, University of Bristol.

MÜLLER, G. 1979. Schwermetalle in den Sedimenten des Rheins — Veränderungen seit 1971. Umschau 79 24:778-783.

RAT VON SACHVERSTANDIGEN FUR UMWELTFRAGEN. 1976. Umweltprobleme des Rheins. 3. Sondergutachten vom März 1976. Stuttgart, Mainz (W. Kohlhammer).

REISS, F. 1968. Ökologische und systematische Untersuchungen an Chironomiden des Bodensees. Ein Beitrag zur lakustrischen Chironomidenfauna des nördlichen Alpenvorlandes. Arch.Hydrobiol. 64:176-323.

SONTHEIMER, H., R. GIMBEL AND W. WEIDEL. 1979. Die Rheinwasserqualität. In: 7. Arbeitstagung der Internationalen Arbeitsgemeinschaft der Wasserwerke im Rheineinzugsgebiet, Basel 29-31 Mai, 1979.

SONTHEIMER, H., A. GLOECKLER AND W. WEINDEL. 1981. Der Rhein in dem Jahren 1980 und 1981. Arbeitsgemeinschaft Rhein-Wasserserke e.V. Jahresbericht 1981. Karlsruhe.

VAN DER VEEN, C. AND J. HUIZENGA. 1980. Combatting river pollution taking the Rhine as an example. Prog. Wat. Tech., 12:1035-1059.

WILSON, R.S. AND J.D. McGILL. 1979. The use of chironomid pupal exuviae for biological surveillance of water quality. Department of the Environment, Water Data Unit Technical Memorandum No. 18.

_____. 1977. A new method of monitoring water quality in a stream receiving sewage effluent, using chironomid pupal exuviae. Water Research 11:959-962.

_____. 1982. A practical key to the genera of pupal exuviae of the British Chironomidae. University of Bristol Printing Office.

Memoirs of The American Entomological Society

1. The Cresson Types of Hymenoptera. Ezra T. Cresson. 1916. $12.00.
3. A Venational Study of the Suborder Zygoptera (Odonata), with Keys for the Identification of Genera. Philip A. Munz. 1919. $10.00.
4. The Blattidae of Panama. Morgan Hebard. 1920. $8.00.
5. The Types of Hymenoptera in the Academy of Natural Sciences of Philadelphia other than those of Ezra T. Cresson. Ezra T. Cresson. 1928. $8.00.
8. The Eumastacinae of Southern Mexico and Central America. James A.G. Rehn and John W.H. Rehn. 1934. $8.00.
9. The Generic Names of the Sphecoid Wasps and Their Type Species. W.S.L. Pate. 1937. $8.00.
10. A Revision of the North American Species Belonging to the Genus Pegomyia. H.C. Huckett. 1941. $6.00.
11. Catalogue and Reclassification of the Nearctic Ichneumonidae. Henry K. Townes, Jr. 1944. $20.00.
13. Elachistidae of North America (Microlepidoptera). Annette F. Braun. 1948. $10.00
14. Classification of the Blattaria as Indicated by their Wings (Orthoptera) John W.H. Rehn. 1951. $10.00.
16. A Taxonomic Study of the North American Licinini with Notes on the Old World Species of the Genus Diplocheila Brulle (Coleoptera). George E. Ball. 1959. $15.00
17. A Taxonomic Study of the Milliped Family Spirobolidae (Diplopoda: Spirobolida) William T. Keeton. 1960. $15.00.
18. The Genus Bucculatrix in America North of Mexico (Microlepidoptera). Annette F. Braun. 1964. $15.00.
19. The Butterflies of Liberia. Richard M. Fox, Arthur W. Lindsey, Jr., Harry K. Clench and Lee D. Miller. 1965. $12.50.
20. A Revision of the Mexican and Central American Spider Wasps of the Subfamily Pompilinae (Hymenoptera: Pompilidae). Howard E. Evans. 1966. $12.50.
21. A Taxonomic and Zoogeographic Survey of the Scarabaeinae of the Antilles (Coleoptera: Scarabaeidae). Eric G. Matthews. 1966. $5.00
22. A Monograph of the Ithomiidae (Lepidoptera) Part III. The Tribe Mechanitini Fox. Richard M. Fox. 1967. $9.00.
23. A List of New North American Spiders, 1940-1966. Beatrice R. Vogel. 1967. $9.00.
24. The Higher Classification, Phylogeny and Zoogeography of the Satyridae (Lepidoptera). Lee D. Miller. 1968. $7.00.
25. The Schizopteridae (Hemiptera: Heteroptera) With the Description of New Species from Trinidad. Michael G. Emsley. 1969. $6.50.
26. A Taxonomic Revision of the Aquatic Beetle Genus Laccophilus (Dytiscidae) of North America. James R. Zimmerman. 1970. $12.00.
27. A Revision of the Nearctic Species of the Tribe Parydrini (Diptera: Ephydridae). Philip J. Clausen and Edwin F. Cook. 1971. $7.00.
28. Tischeriidae of America North of Mexico (Microlepidoptera). Annette F. Braun. 1972. $7.00.
29. The Shield-backed Katydids of the Genus Idiostatus. David C. Rentz. 1973. $9.50.
30. The Systematic and Morphology of the Nearctic Species of Diamesa Meigen, 1835 (Diptera: Chironomidae). Dean Cyrus Hansen and Edwin F. Cook. 1976. $10.00.
31. The Stoneflies (Plecoptera) of the Rocky Mountains. Richard W. Baumann, Arden R. Gaufin and Rebecca F. Surdick. 1977. $10.50.
32. The Genus Isoperla (Plecoptera) of Western North America; Holomorphology and Systematics, and a New Stonefly Genus Cascadoperla. Stanley W. Szczytko and Kenneth W. Stewart. 1979. $7.50.
33. Revision of the Milliped Genus Sigmoria (Polydesmida: Xystodesmidae). Rowland M Shelley. 1981. $11.00
34. Proceedings of the 8th International Symposium on Chironomidae. Jacksonville, Florida, July 25-28, 1982. 1983. $25.00.

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A RECONSIDERATION OF THE MILLIPED GENUS *SIGMORIA*, WITH A REVISION OF *DELTOTARIA* AND AN ANALYSIS OF THE GENERA IN THE TRIBE APHELORIINI (POLYDESMIDA: XYSTODESMIDAE)

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A RECONSIDERATION OF THE MILLIPED GENUS SIGMORIA, WITH A REVISION OF DELTOTARIA AND AN ANALYSIS OF THE GENERA IN THE TRIBE APHELORIINI (POLYDESMIDA: XYSTODESMIDAE)

BY

ROWLAND M. SHELLEY[1]

AND

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INTRODUCTION

This paper reviews the genera in the xystodesmid milliped tribe Apheloriini (Xystodesminae) and provides diagnostic statements for those deemed valid. For *Sigmoria,* which is considered valid since the concepts of the older genus-group names, *Apheloria and Brachoria,* have not been critically analyzed, we present an expanded diagnosis, descriptions of 10 new species, redescriptions of five species, supplemental accounts of 15 species transferred into the genus, and additional information on distribution, ecology, and relationships. *Sigmoria* now consists of 65 species, with three divided into a total of nine subspecies. For *Deltotaria* we present a diagnosis, accounts of the gonopods of the two species in "sigmoid" ter-

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minology[3], diagnoses of the two subspecies of the type species, and distribu-
tional and ecological information. The paper concludes with analyses of the
Apheloriini and the four principal xystodesmid tribes in eastern North
America.

We use five taxonomic categories throughout this work in reference to the
Apheloriini: genera, subgenera, species groups, species, and subspecies. In
various respects their usages are not traditional to xystodesmid classifica-
tions, and explanations are in order.

Genera are taxa with apparent geographic and lineage independence.
Among the Apheloriini, *Sigmoria* is a cohesive geographic entity and forms
a "mosaic" of largely allopatric or parapatric parts (subgenera, species
groups, species, and subspecies). The other genera form their own mosaic
patterns, which overlie each other and *Sigmoria* to varying degrees. Accept-
ance of this minimal generic concept allows us to remain within traditional
limits of xystodesmid classification, because no clear autapomorphies have
yet been found among gonopodal or somatic characters for many genera in-
cluding *Sigmoria,* and there may be none. Consequently, it is geographic
cohesiveness that gives these genera their apparent individuality or reality,
which in turn justifies generic distinction. *Deltotaria,* however, is defined by
an autapomorphy, the coxal apophysis. Thus, *Deltotaria* and *Sigmoria* are
distinct, sympatric geographic entities, but only the former is defined
cladistically.

Subgenera are not customarily employed in milliped classifications, and
we do not advocate their use. However, our analysis of *Sigmoria* resulted in
the recognition of eight major components, all of which have published
genus-group names available. It is convenient to recognize these major en-
tities, and we conserve the senior name at the subgeneric level. The
subgenera may have one or more species groups, tend to be allopatric or
parapatric, do not show clear patterns of lineage independence, and are dif-
ficult to relate in standard cladistic fashion. Lack of lineage independence is
reflected by similarities (symplesiomorphies) between proximal elements of
adjacent subgenera, which we think reflect ancestral continuities. This pat-
tern is a prime reason why the major components are not separate genera;
they are sections of a single geographic entity. We are convinced that seven
subgenera are monophyletic; *Sigiria,* however, may be paraphyletic. Begin-

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[3]The term "sigmoid" has no taxonomic value and refers collectively to the various
apheloriine taxa whose gonopodal acropodites curve in a vaguely sigmoidal fashion. To stand-
ardize taxonomic treatments and to facilitate comparisons between species, Shelley (1981a)
developed new terminology for these acropodites and divided them into sections or zones. This
method of characterizing apheloriine acropodites has been used in subsequent papers and for
simplicity is referred to as "sigmoid" terminology.

ning with the first subgeneric account, that of *Rudiloria,* subgeneric assignment is indicated throughout the text either before or after the specific name, as for example *"ainsliei (Falloria)."* When two or more species in sequence belong to the same subgenus, the designation follows the last — thus *"pela, brooksi,* and *coronata (Dixioria)."*

Species groups combine closely related species, some of which might unite as superspecies or even prove to be conspecific. They are geographically coherent and represent our estimates of specific relationships. In most cases these groups differ considerably from those proposed by Shelley (1981a).

Species are taxa which we hypothesize to be reproductive isolates, apparently segregated from geographically proximal taxa and not connected by intergrades. Evidence for separation comes in various forms. Ranges may be so proximal that discontinuities are abrupt, as between *pela* (Chamberlin) and *wrighti* Hoffman, and *translineata* Shelley and *lyrea* Shelley. Phenotypically different taxa such as *brooksi* Hoffman and *coronata* (Hoffman) that appear to be syntopic in part of their ranges also are considered reproductively isolated. Additionally, there may be a clear range disjunction between taxa that otherwise could be considered subspecies, the chief example being that of *rubromarginata* (Bollman) and *austrimontis* Shelley. Despite their residual intergrades, we consider both full species because genetic interchange is no longer possible; hence, the latter is elevated to specific status. The gap between *leucostriata* Shelley and *xerophylla* Shelley is occupied by several other taxa, and we consider this further evidence for reproductive isolation.

Subspecies are taxa which are reasonably homogeneous throughout their ranges but which connect with other such taxa through intergrade or intermediate forms. We reserve this category for *latior* (Brolemann), *trimaculata* (Wood), and *nigrimontis* (Chamberlin), geographically varied but clinally continuous species with uninterrupted ranges where gene flow is still possible.

The systematic treatment of *Sigmoria* in Part I proceeds in the clockwise geographic sequence of north to south to west, both among the subgenera and their component species groups. Species accounts vary. A few new records are presented for those previously discussed (Shelley 1981a), but otherwise they are merely listed. The new species are described; *houstoni* Chamberlin and *mimetica* (Chamberlin) are redescribed; and the treatments of the transferred species vary according to the depths of previous accounts, some being redescribed, some having gonopodal descriptions in "sigmoid" terminology, and others merely summarized. A new name is proposed for *Sigmoria simplex* Shelley, 1981a, to avert homonymy with *Croatania*

simplex Shelley, 1977. Full synonymies are provided for the newly incorporated species; synonyms of previously included taxa are found in Shelley (1981a). To facilitate identifications we provide anatomical keys to subgenera and species of *Sigmoria* and a tabular presentation (Table 3) of geographical distributions for species of *Sigmoria* and *Deltotaria*. The keys refer to illustrations in this paper plus Shelley (1980a, 1981a and b, 1982, 1983a, 1984a); the table includes a color pattern code.

Holotypes of all pertinent nominal species were seen except those of *Polydesmus trimaculatus* (Wood), which is lost; *Fontaria lutzi* Jacot, for which clear illustrations and reasonably proximal material are available; and *Hubroria picapa* Keeton, *Fontaria pela* Chamberlin, and *Dixioria dactylifera* Hoffman, for which paratypes are available. Two requests to the NMNH failed to produce the holotype of *H. picapa,* which Keeton claimed to have deposited there both in his 1960 paper and in a 1976 letter to the senior author. He kindly loaned paratypes from his collection, and after his death in 1980, these were deposited in the FMNH and the personal collection of R.L. Hoffman. Type specimen notations are always of the senior synonym. Unless otherwise stated in the locality listings, collections were made by the senior author and assistants. The acronym GSMNP denotes the Great Smoky Mountains National Park; acronyms of sources of preserved study material cited in the text are as follows:

AMNH — American Museum of Natural History, New York, NY.

ANSP — Academy of Natural Sciences, Philadelphia, PA

AU — Department of Zoology and Entomology, Auburn University, Auburn, AL

FMNH — Field Museum of Natural History, Chicago, IL

FSCA — Florida State Collection of Arthropods, Gainesville, FL

MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA

NMNH — National Museum of Natural History, Smithsonian Institution, Washington, DC

NCSM — North Carolina State Museum of Natural History, Raleigh, NC. The invertebrate catalog numbers of material from this collection are indicated in parentheses.

PMNH — Peabody Museum of Natural History, Yale University, New Haven, CT

RLH — Private collection of Richard L. Hoffman, Radford, VA

ROM — Royal Ontario Museum, Toronto, Ontario, Canada

RVC — Private collection of the late Ralph V. Chamberlin, now being accessioned by the NMNH.

UMN — Department of Entomology, Fisheries, and Wildlife, University
    of Minnesota, St. Paul, MN
WAS — Private collection of William A. Shear, Hampden-Sydney, VA

LITERATURE REVIEW

The papers pertaining to the species of *Sigmoria* in previous works
(Shelley 1981a, 1983a) were discussed at those times; here major references
on the additional taxa are summarized. The history of *Deltotaria* was
reviewed by Hoffman (1961), the only additional citation being his (1979)
inclusion of it in the tribe Apheloriini, where he said it consisted of five
species in the southern Appalachian region.

The oldest species discussed herein, *trimaculata* Wood (1864, 1865), is
one of four originally placed in *Fontaria* Gray (1832)[4]. One other, *F. rileyi*
Bollman (1888), was proposed in the 19th century, and Chamberlin
(1918a,b) added *F. mimetica* and *F. pela.*

In 1921 Chamberlin erected *Apheloria* for the new species *ainsliei* and *F.
montana* Bollman, which was designated type species. Both were included
under *Apheloria* by Chamberlin and Hoffman (1958), but Hoffman (1978a)
observed that the genus was heterogeneous in its original proposal. Conse-
quently, he removed *ainsliei* from *Apheloria* but left it unassigned. We
agree with Hoffman's assessment and herewith place the species in
Sigmoria.

In 1938 Jacot described *F. lutzi* from Keene, New Hampshire. A year
later the number of pertinent nominal taxa increased dramatically, when
Chamberlin (1939) proposed *A. keuka,* here placed in synonymy under the
nominate subspecies of *trimaculata,* and the genera *Sigmoria, Sigiria,* and
Cleptoria, with seven, one, and two species, respectively. Shelley (1981a)
dealt with *Sigiria* and the species originally assigned to it and *Sigmoria,* and
we can now report that *C. macra* Chamberlin is also properly assigned to
the latter because its characters grade into those possessed by more
"typical" forms. *Cleptoria* therefore becomes a subgenus of *Sigmoria.* Its
second original species was *rileyi,* which Chamberlin (1939) transferred
from *Fontaria.*

The decade of the 1940's brought more nominal species and the initial ef-
fort at reduction through synonymies. Chamberlin (1943) described
Sigmoria houstoni from, supposedly, Houston, Texas, but it actually oc-
curs in the Cumberland Plateau of southern Tennessee. Loomis (1943) sug-

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[4] Because of the extreme confusion surrounding this name, we agree with Hoffman (1979)
that *Fontaria* should be placed on the list of officially rejected names in zoology.

gested that *C. macra* was a synonym of *rileyi* and expressed doubt about the validity of *Cleptoria,* a most perceptive insight that we now agree with. Loomis' insight into relationships showed again in 1944, when he described *C. shelfordi.* He realized 40 years ago that this form was congeneric with *macra,* something that neither Hoffman (1967) nor Shelley (1980a, 1981b) perceived. Chamberlin (1947) proposed *Dixioria* for the new species, *dentifer,* which Hoffman (1956a) correctly synonymized with *pela,* in turn transferred from *Fontaria.* In 1949 Chamberlin described *Apheloria tortua;* and Hoffman added *A. antrostomicola, kleinpeteri,* and *picta,* four Virginia locality records for *trimaculata,* which Attems (1938) had transferred into *Apheloria,* and *Deltotaria coronata.*

The decade of the 1950's featured the Checklist, three papers by Hoffman, and one by Causey. Hoffman, (1950) summarized *Sigmoria,* which included the transfer of *mimetica* from *Fontaria,* and remarked that the absence of gonopodal drawings hampered determination of its generic position. However, he did not provide any, and *mimetica* still has not been illustrated. Hoffman (1951) identified four races of *Apheloria trimaculata* based on the shape and size of the middorsal spot. *Fontaria lutzi* was synonymized with the nominate subspecies, and *A. antrostomicola* and *A. tortua* were reduced to subspecific status. The fourth subspecies, *A. t. incarnata,* occurring in Ontario, Canada, was newly diagnosed. Causey's sole contribution to *Sigmoria* came in 1955, when she established the genus *Rudiloria* for the new species *mohicana.* Hoffman (1956a) transferred *Deltotaria coronata* into *Dixioria* and recognized two species: *dactylifera,* and *pela,* the latter with six subspecies. Chamberlin and Hoffman's checklist of the North American fauna (1958) listed without change the species from all previous studies except the last.

Keeton (1960) began the ensuing decade with the erection of *Hubroria* for the new species, *picapa.* The only other pertinent study of this period was the revision of *Cleptoria* by Hoffman (1967). He recognized five species — *marca; rileyi,* with two subspecies; *abbotti* and *bipraesidens,* both newly diagnosed; and *divergens* (Chamberlin) — and transferred *shelfordi* out of the genus but left it unassigned.

Recent contributions to the taxa under study include the diagnosis of *Apheloria guyandotta,* the transferral of *mohicana* into that genus, and the suppression of *Rudiloria* by Shear (1972). Hoffman (1979) assigned *Apheloria, Sigmoria, Cleptoria, Dixioria,* and *Hubroria,* to the new tribe Apheloriini along with *Croatania,* which Shelley (1977) established for four species in the Carolinas. *Rudiloria* was considered a synonym of *Apheloria* by Hoffman (1979), the most recent action on that taxon, although Hoffman (1978a) had revived it for 10 nominal species of *Apheloria.* The order

of appearance of these two studies was reversed by publication delays. More recently Shelley (1980a) erected *Brevigonus* for *shelfordi* and (1981b) added a second species, *arcuatus*. Shelley (1981a) published a monograph on *Sigmoria* transferring *houstoni* and *mimetica* out of the genus but leaving them unassigned. In the final relevant work, Shelley (1983a) returned *divergens* to *Sigmoria*.

Tourism (Santee State Park); Tennessee Department of Conservation (Cedars of Lebanon, Edgar Evins, Fall Creek Falls, Henry Horton, and Lake Radnor State Parks); the Parks and Historic Sites Division, Georgia Department of Natural Resources (Augusta Canal, Crooked River, Hard Labor Creek, Kolomoki Mounds, and Mistletoe State Parks); the State Parks Division, Alabama Department of Conservation and Natural Resources (Chattahoochee and Chewacla State Parks); and the Division of Recreation and Parks, Florida Department of Natural Resources (Torreya State Park). Cathy Wood typed and retyped the manuscript, and Renaldo G. Kuhler, NCSM scientific illustrator, prepared Figures 5, 14, 19, 25, 28, 32, 38, 42, 46, 61, 64, 70, 74, 78, 85, 89, 93, 98, 100, 106, 110, 116, 122, 128, 138, and 142. Henrik Enghoff (Zoologisk Museum, Copenhagen) and Peter Mundel (NMNH) provided valuable criticism throughout the manuscript; Mary Mikevich and Michael Schauff (Systematic Entomology Laboratory) added comments on the chapters on relationships. Lastly, the senior author wishes to express his deep gratitude to certain colleagues at the NCSM, who have both supported and encouraged his basic taxonomic research on millipeds throughout his employment. Financial support for this research was rendered in part by the National Science Foundation Grants Nos. DEB 7702596 and 8200556, and was used to fund necessary travel and subsistence, employment of field assistants, and publication costs.

PART I.   REVISION OF SIGMORIA
by Rowland M. Shelley

Taxonomic Characters

The taxonomically important characters of *Sigmoria* are as listed previously (1981a), but with the inclusion of more species, they require elaboration. Most of these characters are found on the male gonopods, and in much of the eastern United States collection of males is mandatory for positive generic determinations. One exception is the northeast (New England, New York, Canada, and northern Pennsylvania and New Jersey), where *trimaculata* and *Apheloria corrugata* (Wood) are the only two apheloriine species. They can be distinguished by color pattern, the former having yellow middorsal spots and the latter displaying yellow metatergal stripes.

Coloration.—   Color and color pattern are useful clues to the identity of an individual of either sex, and I (1981a) presented a table that now must be enlarged (Table 1). As before, all forms display a black metatergal base color and colored paranota, but a middorsal spot pattern is added to the

TABLE 1.   Colors and color patterns of species and subspecies of *Sigmoria*

Pattern	Color	Taxa
Paranotal spots only	red, orange, or yellow	*stenoloba, latior latior,* some *latior* intergrades*, *simplex**
	red only	*australis*, macra, shelfordi, arcuata, robusta, abbotti, rileyi, saluda*
	yellow only	*catawba, simplex*, pela, dactylifera, brooksi, acuminata, coronata, watauga, wrighti*
Paranotal and mid-dorsal spots	both yellow, interior of latter sometimes tinted with red	*guyandotta, trimaculata*
Paranotal spots and metatergal stripes	both yellow to orange	*inornata*, areolata, latior munda*,* some latior intergrades*, *simplex**
	both lemon yellow	*whiteheadi*
	both orange	*planca*
	both red	*inornata*, truncata, sigirioides, quadrata, laticurvosa, stibarophalla, latior munda*, latior hoffmani,* some latior intergrades*, *rubromarginata, triangulata, nigrimontis, australis*, divergens, austrimontis, persica, serrata, bipraesidens, haerens, divaricata, thrinax*
	both violet or purple	*stenogon, disjuncta*
	both white or light yellow	*leucostriata*
	paranota red, stripes blue	*fumimontis, bidens, translineata, lyrea, tuberosa, xerophylla, ainsliei, aphelorioides, prolata, mimetica, crassicurvosa, pendulata, picapa, forficata, houstoni, abbreviata*
	paranota red, stripes white	*nantahalae*

*taxa that are polymorphic for color

several stripe and paranotal spot patterns of before. The last category is also expanded, since some species display only red or yellow paranota in addition to the highly variable colors of *latior latior* and *stenoloba*. In addition to the color variation sometimes seen along the inner margin of the paranotal spots and metatergal stripes, the size of the middorsal spots in *guyandotta* and *trimaculata* varies from small discrete dots, as found in northern populations of the latter, to large semilunar blotches that may even spread laterad into diffuse, indistinct stripes connecting with the paranota markings. To avoid confusion, these species are listed only in the "paranotal and middorsal spots" category, but this variation should be noted because it demonstrates how spot and stripe patterns relate to each other. Table 1 summarizes the most common colors and color patterns for each species and subspecies of *Sigmoria,* omitting occasional variations exhibited by such taxa as *bidens, translineata, divergens, ainsliei, mimetica,* and *pendulata*. Taxa that are commonly polymorphic for color and/or pattern are indicated by an asterisk. A clear paranotal spot and metatergal stripe pattern is evident on preserved material of *mohicana* and *rigida,* but since the colors are unknown, they are omitted. I have not personally collected them, and there is no indication of living colors in either the literature or on labels with the specimens.

The various colors and patterns tend to cluster throughout the range of *Sigmoria* and also within that of the Apheloriini (Figs. 148-150, 159). These phenomena are discussed in Part V.

Sterna.—   Except for the more densely pilose condition in *tuberosa, the* only aspects of the sterna that aid in determinations are the configuration and degree of development of the process of the 4th sternum and, to a lesser extent, those of the 5th. Variation of the processes is as described previously (Shelley 1981a), and Table 2 presents updated information on that of the 4th sternum. The newly included species add to each of the three columns to bring the totals to 37 species in which the process is shorter than the widths of the adjacent sterna, 19 in which they are subequal, and 9 in which the projection is longer.

Gonopodal Characters.—   Most of the specific characters in *Sigmoria* obtain in aspects of the male gonopods. The newly included species increase the scope of variation and require supplemental accounts for each zone of the acropodite plus ones on thickness, the *in situ* arrangements, and the prefemoral process.

1.   *In situ arrangements.—*   The *in situ* arrangements of the newly included species fit, for the most part, the overlapping, crossing, and parallel patterns described previously, although a telopodite will occasionally be dislodged giving an atypical arrangement. The only new configurations oc-

TABLE 2. Length of process of 4th sternum in males in species of *Sigmoria*

Shorter (than widths of adjacent coxae)	Subequal	Longer
latior	*quadrata*	*tuberosa*
stenoloba	*laticurvosa*	*catawba*
areolata	*translineata*	*saluda*
stibarophalla	*lyrea*	*yemassee*
inornata	*fumimontis*	*forficata*
truncata	*ainsliei*	*abbotti*
sigirioides	*aphelorioides*	*arcuata*
stenogon	*bidens*	*robusta*
nantahalae	*macra*	*bipraesidens*
leucostriata	*rileyi*	
xerophylla	*shelfordi*	
rubromarginata	*pela*	
austrimontis	*brooksi*	
triangulata	*acuminata*	
whiteheadi	*coronata*	
nigrimontis	*wrighti*	
disjuncta	*watauga*	
prolata	*haerens*	
mimetica	*trimaculata*	
crassicurvosa		
pendulata		
picapa		
abbreviata		
houstoni		
australis		
simplex		
divergens		
dactylifera		
mohicana		
rigida		
guyandotta		
planca		
persica		
agrestis		
serrata		
divaricata		
thrinax		

cur in *ainsliei, aphelorioides,* and the subgenera *Rudiloria* and *Dixioria.* In *ainsliei* the acropodites intertwine (Fig. 89), which is really a manifestation of the overlapping pattern caused by the circular configuration. Conversely, in most males of *aphelorioides* the acropodites lie above and below each other (Fig. 85) and rarely overlap. In the subgenus *Rudiloria* the telopodites are oriented differently on the coxa and face mediad. Here and in *Dixioria* they are directed transversely across the body and tend to insert in the opposite side of the aperture instead of extending over the anterior margin and lying between the 7th legs. This arrangement is shown in Figures 5 and 14, in Shear (1972, Fig. 1) for *guyandotta,* and in Hoffman (1978, Fig. 2) for *t. trimaculata.*

    2.   *Prefemoral process.*—   With more species and more diversity, the prefemoral process loses all effectiveness as a specific criterion. A basally divided process occurs in four species rather than two (*ainsliei, forficata, translineata,* and *lyrea*), and the configuration in *bidens* is approached in proximal populations of *prolata.* Thus, even in these cases, determinations based solely on the process are inadvisable. Moreover, species are now known without a process or with only a vestige — *pendulata, bipraesidens, rileyi, guyandotta* and *mohicana.*

    3.   *Characters of the acropodite. a) Thickness.*—   The newly added species included those with the heaviest, most massive gonopods in the genus (*rileyi, abbotti, bipraesidens, robusta, crassicurvosa,* and *pendulata*). In a few, such as *mohicana, trimaculata, pela,* and *wrighti,* the acropodites are rather thin and fragile, and similar to those of *stenogon* and *sigirioides.* The others fall between these extremes.

    b) General curvature. — It is in general curvature that the newly added species depart the most from those previously included in *Sigmoria,* and the generic concept must now be broadened to encompass forms whose acropodites circumscribe a complete or nearly complete loop. Three species are involved: *ainsliei, aphelorioides,* and *trimaculata.* In these the anterior bend and apical curve are more or less continuous through the peak, so that the acropodal regions are obscure. The overall configuration is of a smoothly continuous circle, with the tip overlapping or nearly overlapping the basal zone in medial view. Futhermore, many of the newly added species do not possess coplanar basal and distal zones. The latter region angles generally laterad from the peak, and is coplanar with the peak in *houstoni* and *picapa.* Heretofore, only *stibarophalla, disjuncta,* and *divergens* had laterally directed distal zones, but this character is also displayed by *australis, prolata, mohicana,* the subgenus *Dixioria,* and certain species of the *translineata* group of the subgenus *Falloria.*

c) Basal zone. — The basal zone has more taxonomic significance than formerly thought. Previously, the tubercles of *tuberosa* were the only modifications of the outer surface of this region, but with the inclusion of the southeastern lowland forms, more specializations are known. The medial edge of the basal zone is deeply emarginate and notched in *catawba* and *saluda* and sinuous to shallowly notched in *simplex* and *yemassee,* and the basalmost projection is enlarged in the first three. *Sigmoria arcuata, rileyi, abbotti, robusta,* and *shelfordi* have a single basal projection that ranges from a large spur to a strong, distinct spine, which may be homologous with the basalmost projection in *catawba, saluda,* and *simplex.* In the *trimaculata* group the basal zone is directed mediad rather than anteriomediad.

d) Anterior bend. — The anterior bend varies from well defined, in species like *brooksi, rigida,* and *australis,* to broad and poorly defined in those with circular acropodites.

e) Peak. — The peak is tilted laterad in the *mimetica* group of *Falloria,* exposing the undersurface in medial view. It is also much thicker in those species with heavy, massive acropodites.

f) Apical curve and distal zone. — As stated earlier, more species are now known with laterally directed distal zones that are not coplanar with basal zones. In *houstoni* and *picapa* the distal zone is actually coplanar with the peak. Extremely short distal zones, coplanar with the basal zones and directed perpendicularly from the peak, are found in five species of the subgenus *Cleptoria.* The opposite extreme is found in *ainsliei* and *trimaculata,* where the region completes the loop of the acropodite and overlaps the basal zone. *Sigmoria shelfordi* joins *truncata* in lacking this section, the acropodite terminating at the distal extremity of the peak. Additional lobes and flanges are found on the distal zones of *pendulata* and *crassicurvosa.*

g) Tip. — Except for variants of such species as *aphelorioides* and *arcuata,* which have reflexed tips, all the newly added taxa have simple, blunt to acute, terminations.

h) Medial flange. — Considerable additional variation is known for the medial flange. It can be located much more proximally and arise well onto the basal zone. In the forms of *Cleptoria* with heavy acropodites it loses some of the laminate character, becoming correspondingly thick and heavy. The ultimate condition obtains in *bipraesidens,* where the flange is not a lamina but a thickening or swelling of the entire medial surface of the peak with the general contours of the flange in *rileyi* when viewed ventrally. In the *mimetica* group the flange is narrow and the peak is tilted laterad, so that in medial view the undersurface is visible and the flange is obscure.

Likewise, the lamella is obscured in medial view in the subgenus *Rudiloria,* because the basal zone which carries it is directed mediad. *Sigmoria ainsliei, aphelorioides,* and *nantahalae* and the subgenus *Dixioria* lack the flange.

i) Tooth. — Additional species with a tooth on the medial margin of the acropodite include *rigida* and the seven species of the subgenus *Dixioria.* Others, like *rileyi, robusta, catawba,* and *saluda* have broadly rounded or triangular distal lobes on the flange, which may represent the tooth. A small, sharp accessory tooth arising from the under surface of the acropodite at or near the location of the marginal tooth is also present in all species of *Dixioria* except *dactylifera.* The tooth or teeth are usually located on the peak but may also be on the distal zone.

j) Lateral flange. — The lateral flange is absent from most newly added species, and in most of the others it is not laminate. In the southeastern species with heavy acropodites (*rileyi, robusta, abbotti, catawba* and *saluda*) it is more lobe-like, more ventrad than laterad, and poorly demarcated from the acropodite stem in the first three, where it forms the highest point of the acropodite arch.

k) Prostatic groove. — The prostatic groove crosses from the medial to the lateral sides of the acropodite at various positions depending on how the telopodite is situated on the coxa and whether or not the peak is tilted.

l) Solenomerite. — In most species of *Sigmoria* the prostatic groove runs along the main stem of the acropodite, avoiding flanges, lobes, and other adornments, and opens terminally at the tip of the distal zone. In the subgenus *Cheiropus,* however, the acropodite is either apically divided or there is a small subterminal structure on which the groove opens. This structure, or the terminal division carrying the groove, is called the solenomerite, and its position and configuration are taxonomically important.

Genus SIGMORIA Chamberlin

Previous gonopodal descriptions and that of the 6th sternum (Shelley 1981a, 1983a) are rewritten to accommodate the newly incorporated species. Other somatic features are unchanged.

Diagnosis. — Coxa without apophysis; acropodite curving in variable sigmoid to coiled or circular configurations, with or without variable flanges, lobes, or teeth on different zones, but always without a transverse groove or cingulum on outer surface.

Description. — Sternum of segment 6 with or without variable convex recession or excavation between 7th legs to accommodate apical curvatures of acropodites.

Gonopods *in situ* with variable configurations; usually with each acropodite extending mediad beyond midline of aperture and over- or under-lapping other acropodite proximal to midlength in midline, curving slightly anteriolaterad over opposite side of aperture then back

over midline with tips curving dorsad and crossing, apical curvatures extending to varying lengths over anterior margin of aperture and sternum of segment 6; some species with acropodites crossing only once in peak or apical curve regions in midline of aperture, apical curves extending anteriad only slightly beyond anterior margin of aperture; others with acropodites not overlapping but medial edges touching or nearly touching in midline and extending anteriad in subparallel arrangement over anterior margin of aperture and sternum of segment 6, apical portions of curvatures in these forms projecting either dorsad or dorsolaterad; still others with acropodites curving dorsad over opposite side of aperture and either touching or approaching opposite coxa and lying in front of and behind each other or curving laterad toward midline and overlapping opposite member. Coxa moderate to large, without apophysis, connected by membrane only, no sternal remnant. Telopodite set terminally on coxa, latter not projecting distad beyond prefemoral region. Prefemur moderate in size, with or without variable prefemoral process, latter ranging from nubbinlike vestige to long, massive structure extending well beyond tip of acropodite, linear to bisinuate, simple or divided basally into two long, nearly equal components, or divided apically and bifurcate. Acropodite thin and fragile to thick and massive, with torsion, curved through one or more vertical planes in vaguely sigmoidal to loosely coiled or circular configurations as seen *in situ* and in medial and lateral views, configurations as follows: basal zone extending subventrad from prefemur; bent sharply or broadly anteriad (anterior bend) from 1/4 to 1/2 of total acropodal length; usually curved sharply or broadly dorsad or laterad apically (apical curve) near 2/3-3/4 length forming arc with variable diameter; portion between anterior bend and apical curve (peak of arch) coplanar with basal and distal zones or bowed mediad and not coplanar with latter regions, flattened or high and gently rounded in medial view, extending to or beyond level of prefemoral process; region forming apical curve (distal zone) varying in length, either projecting nearly directly dorsad, curved inward into acropodite arch and essentially coplanar with basal zone, or bent abruptly laterad, curving through more than one vertical plane, and not coplanar with basal zone, occasionally coplanar or nearly coplanar with peak, either of subequal width throughout most of length (except apically) or tapering smoothly and continuously to acuminate tip. Basal zone variable in length, inner surface usually directed anteriad, occasionally mediad, with or without variably laminate flange on medial surface and adornments on outer surface, latter including densely packed tubercles, a row of dentate spurs, or single basal spines; medial edge usually entire, occasionally variably expanded and finely scalloped or deeply and irregularly notched; lateral edge occasionally expanded and lamellate. Peak of arch variable in length and width, usually with inner surface directed toward arch, occasionally tilted laterad and facing mediad, with or without flange of variable length, width, and configuration on medial edge, arising from proximal part of basal zone to proximal part of peak, usually terminating from near midlength of peak to proximal part of distal zone, with or without variable laminate to spiniform tooth arising from medial edge or outer surface distal to flange, separated to varying lengths from flange, occasionally fused to latter; occasionally with small, sharp accessory tooth on undersurface at level of marginal tooth. Distal zone present or absent; when present with or without variable flanges or lobes proximally on both medial and lateral sides, one or both often arising on distal extremity of peak and distally on medial side; also with or without long, narrow, laminate flange on lateral side, arising near beginning of apical curve, terminating proximal to tip, flange occasionally modified into subtriangular lobe, long narrow subrectangular projection, or greatly enlarged and swollen, forming outermost point on acropodite arch; usually without but occasionally with teeth; when absent sometimes replaced by variably positioned solenomerite, best viewed laterally. Termination variable; either blunt or acuminate unmodified end of peak or distal zone; or small, reflexed lamina on medial edge directed at sharp angle (often perpendicularly) from distal zone; termination occasionally angled from distal zone but not separated into distinct lamina. Prostatic groove arising in pit

on prefemur, running along stem of acropodite and crossing from medial to lateral sides at various locations, opening terminally on tip of distal zone or on reflexed lamina when present.

Females agreeing essentially with males in somatic features, except paranota usually more strongly depressed, creating appearance of more highly arched or vaulted body.

Distribution. — As currently understood (Fig. 145), *Sigmoria* occupies a large, contiguous, irregular area and five smaller, disjunct ones. The former extends from Ontario and northern New England to northeastern Florida, and longitudinally from the outer coastal Plain of the Carolinas and Georgia, the Blue Ridge Province of Virginia, and the New England Province, to piedmont Georgia, the Ridge and Valley Province of Tennessee, and Central Ohio. One disjunct area encompasses most of the Cumberland Plateau,[5] eastern Highland Rim, and Nashville Basin of Tennessee.[6] Another is located mostly in the Coastal Plain of south-central Alabama, ranging northward slightly into the Fall Zone. The third spans the Chattahoochee and upper Appalachicola Rivers in the Coastal Plains of southwestern Georgia, southeastern Alabama, and the adjacent part of Florida; and the fourth is located in extreme southern Georgia and the northern part of peninsular Florida. The fifth disjunct area, in the Cumberland Plateau of north-central Alabama and shown by the dot, is represented by a single male of *rileyi,* which became available as the paper was being drafted. The lacunae in Tennessee and those between the more southern disjunct areas are slightly over 40 miles wide and may be sampling artifacts that will eventually be joined. However, I have not found representatives there in nearly 10 years of field work and show them to accurately depict present knowledge. The blank area in south-central Georgia is around 90 miles in diameter and though nearly surrounded by *Sigmoria,* seems likely to survive additional field work. *Sigmoria* thus inhabits seven physiographic provinces and 17 states plus Ontario. The total north-south length is over 1,000 miles, and that from the Atlantic Ocean to central Tennessee is around 550 miles. The Alabama River seems a likely western distributional limit in Alabama.

Species. — Sixty-five, with three consisting of nine geographic races.

KEY TO SUBGENERA OF SIGMORIA

1.   Color of metatergal stripes contrasting with that of paranota or both either white or pale
         yellow . . . . *Falloria* Hoffman
      Metaterga either uniformly black, variably spotted middorsally, or with stripes concolorous with paranota but not white or pale yellow 2

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[5] The local name, Cumberland Plateau, is used in this paper to refer to the southern part of the Appalachian Plateaus Physiographic Province.

[6] The Nashville Basin and the surrounding Highland Rim are the southernmost sections of the Interior Low Plateaus Physiographic Province.

2.   Gonopods *in situ* with acropodites extending mostly mediad and projecting over opposite side of aperture, occasionally with sides tilted and leaning over anterior margin   3
      Gonopods *in situ* with acropodites extending mostly anteriad, projecting well beyond anterior margin of aperture and inserting between legs of segment 6   4
3.   Caudolateral corners of paranota rounded through midbody segments; acropodite usually with accessory tooth arising from undersurface at or distal to level of tooth; metaterga uniformly black, never with spots or stripes . . . . *Dixioria* Chamberlin
      Caudolateral corners of paranota rounded only on anteriormost segments; acropodite without accessory tooth; color variable, metaterga usually with spots and stripes . . . . *Rudiloria* Causey
4.   Acropodites either with distal zones curving strongly laterad and obscured in medial view by stems or medial flanges, or with variably positioned solenomerites replacing distal zones . . . . *Cheiropus* Loomis
      Acropodites without solenomerites; distal zones visible in medial views   5
5.   Acropodites usually massive and heavily sclerotized; basal zones usually with variable spines or teeth on outer or medial surface   6
      Acropodites thin and fragile to moderate, never massive; basal zones without modifications   7
6.   Basal zones with variable teeth or variably notched expansions on proximomedial edges; prefemoral processes large to enormous, usually extending beyond tips of acropodites . . . . *Croatania* Shelley
      Basal zones with at most a single spine on outer surfaces; prefemoral processes small to absent . . . . *Cleptoria* Chamberlin
7.   Acropodites either with reflexed tips or with this general configuration . . . . *Sigmoria* Chamberlin
      Tips of acropodites simple, blunt to acuminate . . . . *Sigiria* Chamberlin

KEY TO SPECIES OF SIGMORIA
(based primarily on adult males)

The difficulty of devising a key to the variable species of *Sigmoria* is greatly magnified by the addition of more congeners than were in the original revision (Shelley 1981a). Even less can now be said about a given species that does not also apply to another, and it is harder to compose couplets so as not to exclude important variants. Qualifying modifiers such as "usually" are therefore found throughout the key, because of the high frequency of exceptional variants. Also necessary are relative comparisons and subjective criteria like thickness, whose utility depends upon one's experience with "sigmoid" xystodesmids. For these reasons and to facilitate usage, most couplets contain more than one comparative criterion. In the following key the three subdivided species are treated as species, so all subspecies and intergrades key out at the same couplet. Except for lateral flanges, most characters of dissected gonopods are best seen in medial view,

particularly those involving comparisons such as "...extending beyond level of distal zone." The few other instances when the lateral perspective is desirable are so stated. Figure numbers and generalized range descriptions are given to enhance the key. To avoid repetition and to distinguish them from drawings in this paper, illustrations in my previous revision (Shelley 1981a) are indicated by an asterisk after the number. References are cited for figures in other papers.

As all species of *Sigmoria* display vivid pigmentation, and the colors and patterns vary considerably, a checklist (Table 3) is presented after the key in which the distribution by state and color pattern is tabulated. Thus, where locality and color are known, determinations may be easier with this table than with the anatomical key. The two complement each other nicely, and the forms of *Deltotaria* are also included in the table for the sake of completion.

1. Gonopods with variably positioned solenomerites, best visible in lateral perspective 59
    Without this character   2
2. Gonopods with variable medial flanges, occasionally vestigial 12
    Without this character   3
3. Acropodite configuration circular, distal zone curving broadly into arch in medial view, extending beyond prefemoral process and overlapping or nearly overlapping basal zone; tooth absent   4
    Acropodite configuration otherwise, either resembling number 7, an inverted L, or curving broadly and continuously to but not beyond level of prefemoral process; tooth present   5
4. Prefemoral process divided basally into two long, unequal components; distal zone coplanar with basal zone (Figs. 90-91); Knox, Sevier, and Blount cos, TN . . . .
    . . . . *ainsliei* (Chamberlin)
    Prefemoral process simple, upright, and acuminate; distal zone curving sublaterad from peak, not coplanar with other sections; (Figs. 86-87); Swain Co. NC, to McMinn Co., TN . . . . *aphelorioides,* new species
5. Acropodite with minute, sharply pointed accessory tooth arising from under surface of acropodite stem or main tooth at or distal to latter   6
    Without this character 11
6. Outer margin of distal extremity of peak greatly expanded into broadly rounded lobe; accessory tooth arising from base of main tooth; prostatic groove crossing to lateral surface at anterior bend; latter sharp, well defined (Figs. 39-40); Washington Co., VA, and Johnson Co., TN . . . . *brooksi* (Hoffman)
    Outer margin of distal extremity of peak at most only faintly expanded, not lobe-like; accessory tooth arising from acropodite stem; anterior bend broad, poorly defined; prostatic groove crossing to lateral side on prefemur (Figs. 20-22, 26, 29-30, 33-36)   7
7. Acropodite configuration a flattened, open arch, overhanging and extending slightly beyond level of prefemoral process; peak linear; distal zone short, terminating well above level of prefemoral process (Figs. 26, 29-30)   8

Acropodite configuration a smooth, continuous curve, arch overhanging and extending slightly beyond level of prefemoral process; peak gently curved and rounded, apex at midlength; distal zone relatively long, extending to or near level of prefemoral process (Figs. 20-22, 33-36) 9

8. Tooth present (Figs. 29-30); Tazewell Co., VA, to Watauga Co., NC . . . .
    . . . . *coronata* (Hoffman)
    Tooth absent (Figs. 26-27); Johnson Co., TN . . . . *acuminata* (Hoffman)

9. Accessory tooth arising distal to tooth, fully visible in medial view (Figs. 35-36); Watauga and Wilkes cos., NC . . . . *watauga,* new species
    Accessory tooth arising at same level as tooth (when present), partly obscured in medial view (Figs. 20-22, 33-34) 10

10. Tooth always present, quadriform, apically dentate (Figs. 33-34); Johnson Co., TN, to Caldwell Co., NC . . . . *wrighti* (Hoffman)
    Tooth present or absent, triangular to spiniform (Figs. 20-24); Carter Co., TN, to McDowell Co., NC . . . . *pela* (Chamberlin)

11. Tooth large, extending in medial view well below level of distal zone and nearly to that of prefemoral process, inner apical corner produced, extending into arch; lateral flange absent (Figs. 43-44); corners of paranota rounded beyond midlength; paranota yellow, metaterga black, without stripes; Ashe Co., NC . . . .
    . . . . *dactylifera* (Hoffman)
    Tooth subequal in length to that of distal zone, but short, barely projecting below peak, terminating well above level of prefemoral process; lateral flange present (Figs. 63-64*); corners of paranota rounded only in anterior half of body; paranota red, metatergal stripes white; Swain Co., NC, to Towns and Union cos., GA . . . .
    . . . . *nantahalae* Hoffman

12. Prefemoral process usually present; occasionally vestigial 18
    Prefemoral process usually absent 13

13. Acropodite of normal or moderate thickness or thin and fragile, latter poorly sclerotized
    14
    Acropodite thick and massive, heavily sclerotized 16

14. Basal zone with basal spine on outer surface (Shelley 1981b, Figs. 3-5); Pickens to Abbeville cos., SC . . . . *arcuata* (Shelley)
    Without this character 15

15. Distal zone flared, lamellate (Fig. 9); Wyoming Co., WV to Menifee Co., KY . . . .
    . . . . *guyandotta* (Shear)
    Distal zone of nearly equal width throughout except for tip, without lamellae (Fig. 11); Ashland Co., OH . . . . *mohicana* (Causey)

16. Peak flat and relatively long, about 1/3 of acropodite length; distal zone relatively short, terminating well above level of prefemur, directed perpendicularly from peak, forming rectangular acropodal arch (Figs. 50-51, 57-58) 17
    Peak short, high, and rounded; distal zone relatively long, terminating at level of prefemoral process, arch an inverted U (Fig. 123); Putnam and Dekalb cos., TN . . . . . .
    . . . . *pendulata,* new species

17. Distal zone relatively broad, sides curving and converging to blunt tip; medial flange thick but distinctly laminate (Figs. 50-51); Clarke Co., GA, to Lee and Jefferson cos., AL . . . . *rileyi* (Bollman)
    Distal zone relatively narrow, inner edge straight, outer curving inward to acuminate tip; medial flange represented by thickening of entire medial surface of peak (Figs. 57-58); Jackson Co., GA . . . . *bipraesidens* (Hoffman)

18. Distal zone and apical curve absent; acropodite terminating at distal extremity of peak
     19
     Distal zone and apical curve present, length and configuration variable   20
19. Medial flange arising on basal zone and terminating on distal extremity of peak; acropo-
     dite relatively thick and heavy, with or without proximal spine on outer edge of
     basal zone, with or without short, acute spur on medial or outer surfaces of peak
     (Shelley 1980a, Figs. 7-12); Oconee to McCormick cos., SC . . . .
     . . . . *shelfordi* (Loomis)
     Medial flange arising on proximal part of peak and terminating just proximal to tip;
     acropodite relatively thin and blade-like, without spines or spurs (Figs. 37-38*);
     Yancey and Mitchell cos., NC . . . . *truncata* Shelley
20. Basal zone with teeth, spines, and/or tubercles on medial or outer surfaces (Figs. 47-48,
     53-54, 62-63, 92-93*; Shelley 1977, Figs. 1, 3-4, 6)   21
     Without these features, surfaces of basal zone smooth   27
21. Proximomedial edge of basal zone expanded and irregular, with small denticulations to
     sharply acute teeth and spines   22
     Medial edge of basal zone smooth and entire, not expanded   25
22. Prefemoral process terminating below level of distal zone (Figs. 47-48); Chester to
     Berkeley cos., SC . . . . *simplex* (Shelley)
     Prefemoral process large, extending to or beyond level of distal zone (Shelley, 1977, Figs.
     1, 3, 6)   23
23. Prefemoral process apically bifurcate (Shelley 1977, Fig. 3); Laurens to Aiken cos., SC
     . . . . *saluda* (Shelley)
     Prefemoral process simple, not bifurcate   24
24. Prefemoral process of approximately uniform width except near tip, bisinuately curved;
     proximomedial expansion of basal zone small and inconspicuous, with only small
     denticulations (Shelley 1977, Fig. 6); Beaufort and Jasper cos., SC . . . .
     . . . . *yemassee* (Shelley)
     Prefemoral process subglobose basally, distal 1/3 narrower and bent into arch; proximo-
     medial expansion broad, irregularly notched (Shelley 1977, Fig. 1); Lincoln Co.,
     NC, to Chester Co., SC . . . . *catawba* (Shelley)
25. Outer margin of basal zone with dense cluster of minute tubercles (Figs. 92-93*); Swain
     Co., NC . . . . *tuberosa* (Shelley)
     Outer margin of basal zone with basal, acute spine   26
26. Distal zone with outer margin continuous with lateral flange (lobe), without indentation,
     sides broadly rounded and converging to blunt tip; medial flange conspicuous, ter-
     minating in rounded lobe (Figs. 62-63); Oconee and Anderson cos., SC . . . .
     . . . . *robusta,* new species
     Distal zone sharply demarcated from lateral flange (lobe) by deep indentation, sides
     gently curved and converging to acuminate tip; medial flange inconspicuous,
     without distal lobe (Figs. 53-54); Hart to Burke cos., GA . . . . *abbotti* (Hoffman)
27. Acropodite with peak tilted laterad, exposing under-surface in medial view; course of
     prostatic groove visible in medial view up to distal extremity of peak or proximal
     part of distal zone (Figs. 111, 117, 120)   28
     Orientation of peak normal or tilted mediad   29
28. Acropodite massive, heavily sclerotized; distal zone with broadly rounded lobe at mid-
     length on medial surface or with terminal medial lamina; tip a short, acuminate, and
     laminate projection from apex of distal zone (Figs. 117-120); Smith and Dekalb
     cos., TN . . . . *crassicurvosa,* new species

Acropodite moderately thick and heavy; distal zone without modifications; inner corner produced to form tip (Figs. 111-112); Robertson to Maury cos., TN . . . .
. . . . *mimetica* (Chamberlin)

29. Prefemoral process divided from base to midlength into two long, prominent, nearly equal components (Figs. 94-96, 99-100, 68-69*, 72-73*).   30
Prefemoral process with or without subterminal spurs or at most only shallowly or apically bifurcate, components small and usually unequal   33

30. Distal zone long, curving broadly well below level of uppermost component and nearly to level of prefemoral division; tip pseudoreflexed (Figs. 72-73*); Swain Co., NC, and Blount Co., TN . . . . *lyrea* Shelley
Distal zone short, terminating above prefemoral components; tip blunt or acuminate
. . . .   31

31. Acropodite with rounded lobe on lateral edge at apical curve, peak tilted mediad exposing lateral margin in medial view; distal zone coplanar with basal zone; tip blunt (Figs. 68-69*); Swain Co., NC, and Blount Co., TN . . . .
. . . . *translineata* Shelley
Acropodite without lobe on lateral margin; orientation of peak normal; distal zone curving generally laterad from peak, not coplanar with basal zone; tip acuminate . . .   32

32. Prefemoral process divided near midlength, components relatively short, straight, and nearly equal; medial flange short and narrow, arising near midlength of peak, margin gently rounded; distal zone short, barely projecting into arch (Figs. 99-100); Bledsoe and Van Buren cos., TN . . . . *abbreviata,* new species
Prefemoral process divided basally, components moderate to long, lateral one broadly or sharply curved ventrad near midlength; medial flange variable, arising from proximal part of basal zone to peak, broadly rounded or triangular on distal extremity of latter; distal zone moderately long, curving well into arch (Figs. 94-96); Scott to Hamilton cos., TN . . . . *forficata,* new species

33. Basal zone with inner surface directed mediad; medial flange narrow located entirely on basal zone, inconspicuous in medial view (Figs. 2, 6, 15)   34
Basal zone with inner surface directed generally anteriad; medial flange with configuration and position variable, not located entirely on basal zone, conspicuous or inconspicuous   35

34. Acropodite with distinct spiniform or triangular tooth near midlength of peak (Figs. 15-16); metaterga with stripes along caudal margins; Kanawha, Clay, and Nicholas cos., WV . . . . *rigida,* new species
Without this character; metaterga usually with variable middorsal spots, occasionally with stripes; Ontario and northern New England to Washington Co., VA
. . . . *trimaculata* (Wood)

35. Prefemoral process long, extending beyond level of distal zone (Figs. 79-83)   36
Prefemoral process terminating well below level of distal zone   37

36. Distal zone curving dorsad (downward in medial view) from peak, coplanar with basal zone; tooth present on proximal part of distal zone, widely separated from medial flange; prefemoral process greatly enlarged to globose basally (Figs. 80-81*); Sevier Co., TN . . . . *bidens* (Causey)
Distal zone directed laterad from peak, not coplanar with basal zone; tooth absent; prefemoral process variable but at most only moderately swollen basally (Figs. 79-83); Sevier Co., TN . . . . *prolata,* new species

37. Distal zone curving generally laterad from peak, not coplanar with basal zone   38

46. Medial flange small, not obscuring stem of acropodite in medial view; distal zone with opposing proximal lobes on medial and lateral margins, lateral lobe larger (Figs. 84*, 88*)... 47)
   Medial flange larger, obscuring at least small section of stem of acropodite in medial view; distal zone either without lobes or with lobe only on lateral side......... 48
47. Portion of distal zone distal to lobes relatively long, bent sharply into arch; lateral flange present (Figs. 84-85*); paranota and metatergal stripes white to light yellow; Cocke and Sevier cos., TN .... *leucostriata* Shelley
   Portion of distal zone distal to lobes relatively short, only slightly curved into arch; lateral flange absent (Figs. 88-89*); paranota red, metatergal stripes blue; McMinn Co., TN, to Gilmer Co., GA .... *xerophylla* Shelley
48. Lateral flange absent 49
   Lateral flange present 51
49. Arch of acropodite subtending a square; peak flattened, length nearly equal to distal zone (Figs. 45*, 47*); Lexington, Saluda, and Edgefield cos., SC...............
   .... *quadrata* Shelley
   Arch of acropodite otherwise; peak gently curved or rising to apex at beginning of apical curve, shorter or longer than distal zone............................... 50
50. Peak of arch gently curved, shorter than distal zone; medial flange relatively short, margin acuminate; distal zone relatively long, projecting dorsad from peak (Fig. 41*); Yancey Co., NC .... *sigirioides* Shelley
   Peak of arch with apex distad at beginning of apical curve, much longer than distal zone; medial flange relatively long and narrow, margin variable; distal zone relatively short, projecting dorsad from peak or curved into arch (Figs. 31*, 33*); Mitchell, Yancey and McDowell cos., NC .... *inornata*, new name
51. Medial flange short, obscuring at most only short section of stem of acropodite; peak of arch rounded, anterior bend and apical curve more or less continuous through peak, poorly defined; distal zone curved but not projecting significantly into arch (Figs. 51*, 53*); Aiken Co., SC .... *laticurvosa* Shelley
   Medial flange longer, obscuring long section of acropodite stem; peak not rounded, anterior bend and apical curve sharp and well defined, not continuous through peak; distal zone curved or straight, projecting well into arch 52
52. Apical curve bisinuate, with two inward bends into arch; lateral flange variable, absent, triangular, or rectangular (Figs. 57*, 59-60*); Transylvania and Henderson cos., NC
   .... *stenogon* Chamberlin
   Apical curve smoothly rounded and continuous, forming arc with variable diameter; lateral flange present, usually long and narrow, occasionally with margin projecting and irregular, never triangular or rectangular 53
53. Acropodite thick and heavy; peak tilted mediad, exposing lateral margin in medial view; tooth absent (Fig. 76*); Blount Co., TN .... *fumimontis* Shelley
   Acropodite moderately thick and heavy; peak oriented normally, lateral edge obscured in medial view; tooth present 54
54. Peak flexed ventrad at midlength; tooth attached to lamina of medial flange but well separated from lobe of latter; tip simple (Fig. 21*); Buncombe Co., NC ....
   .... *areolata* Shelley
   Peak relatively flat; tooth present or absent, not attached to lamina of medial flange; tip reflexed 55
55. Medial flange narrow, poorly demarcated from stem of acropodite, depth much less than that of apical curvature; when present, tooth usually well separated from

medial flange, often greatly reduced and rounded (Figs. 12-15*); Wilkes and
Catawba cos., NC . . . . *stenoloba* Shelley
Medial flange broad to large, well demarcated from stem of acropodite; depth equal to
or greater than that of apical curvature; when present, tooth located at distal ex-
tremity of medial flange, usually subacuminate (Figs. 3*, 8*, 9*); southern West
Virginia to southern South Carolina . . . . *latior* (Brolemann)
56. Distal zone tapering to acuminate tip; medial and lateral flanges large and conspicuous;
peak of arch gently rounded (Figs. 97*, 105*) 57
Distal zone of nearly equal width throughout except for tip; latter blunt; flanges reduced,
medial often vestigial; peak either curved or flattened (Figs. 108-112*, 114-121*,
123-124*, 126-127*); Greene and Unicoi cos., TN, to Buncombe and McDowell
cos., NC . . . . *nigrimontis* (Chamberlin)
57. Lateral flange triangular, located entirely on peak; distal zone bisinuately curved distad,
directed toward prefemoral process (Fig. 105*); Cocke Co., TN, and Madison
Co., NC . . . . *triangulata* Shelley
Lateral flange with margin broadly rounded, occurring from distal extremity of peak to
midlength of distal zone; latter bent sharply inward into arch at termination point of
flanges (Figs. 97*, 100*, 102*) 58
58. Acropodites in medial view showing profile of arch and distal zone; edge of medial flange
visible in medial view, face directed anteriad; prefemoral process relatively long,
recurved at midlength and directed toward distal zone, simple or bifurcate with one
component usually much longer (Fig. 97*); Sevier and Cocke cos., TN, to Tran-
sylvania Co., NC . . . . *rubromarginata* (Bollman)
Distal zone twisted mediad revealing part of face of medial flange or all of faces of medial
and lateral flanges in medial view; proximal portion of arch visible, distal obscured
by flanges; bend of distal zone partly or completely obscured by flanges in medial
view; prefemoral process variably short and straight, usually bifurcate with sube-
qual components (Figs. 100-103*); Buncombe to Burke cos., NC . . . .
. . . . *austrimontis* Shelley
59. Acropodite with row of distinct spurs on basal zone (Shelley 1982, Figs. 4, 8, 12) 60
Without this character 62
60. Acropodite apically trifurcate, solenomerite directed away from gonopod along axis of
acropodite; latter a broad, continuous curve, anterior bend poorly defined (Shelley
1982, Figs. 11-12); Polk and Henderson cos., NC . . . . *thrinax* (Shelley)
Acropodite apically blunt to subacute, with at most two terminal projections; soleno-
merite located beneath distal extremity of peak, directed perpendicularly and laterad
to peak; acropodite bent sharply at 1/3 to 1/2 length, anterior bend well defined
. . . . 61
61. Solenomerite fused to undersurface of peak; spurs moderate in size, located entirely on
basal zone (Shelley 1982, Figs. 3-4); McDowell, Buncombe, and Henderson cos.,
NC . . . . *haerens* (Shelley)
Solenomerite a separate bisinuate process, narrowly segregated from peak; spurs
moderate to large in size, extending around anterior bend to base of lateral flange on
peak (Shelley 1982, Figs. 7-8); Rutherford, Henderson, and Polk cos., NC
. . . . *divaricata* (Shelley)
62. Acropodite broadened distad into cupulate expansion or cap; solenomerite either beneath
and partly or completely obscured by cap, or located laterad at its base 63
Acropodite relatively narrow; widest basally, tapering smoothly to acuminate tip;
solenomerite about half the length of acropodite, arising near base of, and running

subparallel to, acropodite (Shelley 1984a, Figs. 10-11); Fall Zone of central Georgia
. . . . *persica* (Hoffman)
63. Solenomerite distinctly visible on lateral side of acropodite at base of expansion; except
for eastern populations, margin of expansion not strongly serrated (Shelley 1984a,
Figs. 3-7); Thomas Co., GA, to Hernando Co., FL . . . . *planca* (Loomis)
Solenomerite located beneath cap and partly or completely obscured; margin of ex-
pansion strongly serrated 64
64. Acropodite in form of continuous, broadly curved arc, extending in medial view beyond
level of prefemur; margin of expansion with a single row of up to 12 teeth;
solenomerite a thickened, sclerotized boss (Shelley 1984a, Figs. 13-15); Charleston
Co., SC, to Clarke and Burke cos., GA . . . . *agrestis* (Loomis)
Acropodite in form of inverted L, stem relatively straight, bent sharply anteriad at level
of cap, overhanging prefemur in medial view; margin of expansion highly serrate,
with two or more rows of variable teeth; solenomerite a thin, falcate projection
tucked under teeth, distal to boss (Shelley 1984, Figs. 19-22); Liberty Co., GA, to
Duval Co., FL . . . . *serrata* (Shelley)

SIGMORIA (RUDILORIA) Causey, new status

Rudiloria Causey, 1955:28. Chamberlin and Hoffman, 1958:47. Jeekel, 1971:285. Hoffman
1978:6

Type species. — Rudiloria mohicana Causey, 1955, by original designa-
tion.

Diagnosis. — Metatergal color pattern variable, with spots or stripes of
varying widths and diameters, at least partly concolorous with paranotal
markings; gonopods *in situ* with acropodites extending mostly over op-
posite side of aperture, not projecting anteriad between legs of segment 6;
acropodites relatively thin and fragile, oriented on coxa with inner surface
directed mediad, with narrow medial flange present on basal zone, largely
undetectable in medial view because of acropodal orientation; tip simple.

Remarks. — Occurring from Virginia to Canada and northern New
England, the subgenus *Rudiloria* occupies the largest and most northerly
range in *Sigmoria s. lat.* At first glance most of the species do not appear
congeneric with *latior (Sigmoria)* or the species formerly described (Shelley
1981a) as having acropodites shaped like the number 7, but the most ex-
treme forms with circular acropodites connect with the latter through a con-
tinuum of intermediate forms and there are important similarities with
known species of *Sigmoria s. lat.* in North Carolina and Tennessee. Over
the years these intermediate forms have received names which I retain, there
being no compelling reason to do otherwise. More collecting is needed in
eastern Kentucky, northern West Virginia, southern and eastern Ohio, and
western Pennsylvania before their true statuses can be determined. In the
only case where ample material is available, *trimaculata* from the counties

TABLE 3. Distribution of species and subspecies of *Sigmoria* and *Deltotaria* by state and color pattern

Code for color pattern:
1. With yellow to red paranotal spots, metaterga entirely black.
2. With yellow to red paranotal spots, metaterga with middorsal spots.
3. With yellow or orange paranotal spots and metatergal stripes.
4. With red paranotal spots and metatergal stripes.
5. With violet or purple paranotal spots and metatergal stripes.
6. With white or pale yellow paranotal spots and metatergal stripes.
7. With red paranotal spots, metaterga with blue stripes.
8. With red paranotal spots, metaterga with white stripes.
9. With yellow or orange paranotal spots, metatergal stripes, and sparkling sheen.
10. Colors and pattern unknown.

Taxon	Code	AL	FL	GA	SC	NC	TN	KY	VA	WV	OH	MD	PA	NY	New England	Ontario
Sigmoria																
(Rudiloria)																
1. *t. trimaculata*	2,3								+	+		+	+	+	+	+
2. *t. kleinpeteri*	2								+	+						
3. *trimaculata* intgds.	2							+	+							
4. *guyandotta*	2									+						
5. *mohicana*	10										+					
6. *rigida*	10									+						
(Dixioria)																
7. *pela*	1					+	+									
8. *acuminata*	1					+	+									
9. *coronata*	1					+	+	+								
10. *watauga*	1					+	+									
11. *wrighti*	1					+	+									

12. *brooksi*	1
13. *dactylifera*	1
(Sigmoria)	
14. *l. latior*	1
15. *l. munda*	3,4
16. *l. hoffmani*	4
17. *latior intgds.*	1,3,4
18. *stenoloba*	1
19. *quadrata*	4
20. *laticurvosa*	4
(Croatania)	
21. *catawba*	1
22. *saluda*	1
23. *simplex*	1,3,4
24. *yemassee*	10
(Cleptoria)	
25. *rileyi*	1
26. *abbotti*	1
27. *bipraesidens*	4
28. *robusta*	1
29. *arcuata*	1
30. *shelfordi*	1
31. *macra*	1
(Cheiropus)	
32. *australis*	1,4
33. *stibarophalla*	4
34. *divergens*	4,5
35. *haerens*	4
36. *divaricata*	4
37. *thrinax*	4

Taxon	Code	AL	FL	GA	SC	NC	TN	KY	VA	WV	OH	MD	PA	NY	New England	Ontario
38. *agrestis*	4			+												
39. *serrata*	4		+	+												
40. *planca*	3		+	+												
41. *persica*	4		+	+												
(Sigiria)																
42. *rubromarginata*	4				+	+										
43. *austrimontis*	4				+	+										
44. *whiteheadi*	3								+							
45. *triangulata*	4					+	+									
46. *n. nigrimontis*	4					+	+									
47. *n. intermedia*	4					+	+									
48. *n. angulosa*	4					+	+									
49. *n. unicoi*	4						+									
50. *sigirioides*	4					+										
51. *truncata*	4					+										
52. *inornata*	3,4					+										
53. *areolata*	3					+										
54. *stenogon*	5					+										
55. *disjuncta*	5			+		+										
(Falloria)																
56. *nantahalae*	8			+		+										
57. *leucostriata*	6				+											
58. *xerophylla*	7			+			+									
59. *apheloroides*	7				+	+										

60. *translineata*	7			+		+
61. *fumimontis*	7					+
62. *lyrea*	7			+		+
63. *ainsliei*	7					+
64. *bidens*	7					+
65. *prolata*	7					+
66. *tuberosa*	7			+		
67. *forficata*	7					+
68. *houstoni*	7					+
69. *abbreviata*	7					+
70. *picapa*	7					+
71. *mimetica*	7					+
73. *pendulata*	7					+
73. *crassicurvosa*	7					+
Deltotaria						
b. *brimleii*	4	+			+	+
b. *philia*	4,9	+	+		+	
brimleii intgds.	4		+			
lea	9			+	+	

of western Virginia, it is possible to combine nominal species to form subspecies and synonyms.

The acropodites of the forms of *Rudiloria* are relatively thin and fragile and curve more mediad than anteriad, thus projecting more over the opposite side of the aperture than over the anterior margin and the 6th sternum. The inner surface of the basal zone is directed mediad, and since the thin, narrow medial flange is located chiefly in this region, it it barely detectable in medial view. The most variable aspect of the acropodites is the distal zone, which can be moderate to very long, overlapping the basal zone and forming a loop or circular acropodite. This condition is similar to that in *ainsliei, aphelorioides, (Falloria)* and species of *Apheloria*. The prefemoral processes range from absent to short and triangular to moderately long and uncinate. The subgenus is comprised of five known forms in a single species group, the *trimaculata* group. Two forms are considered races of a single species.

Components. — *trimaculata* (Wood) [*t. trimaculata, t. kleinpeteri* (Hoffman)], *mohicana* (Causey), *guyandotta* (Shear), *rigida* new species.

Sigmoria (Rudiloria) trimaculata (Wood), new combination

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on distal part of basal zone and with variable color pattern, paranota yellow, metaterga with yellow, red, or orange markings on caudal edges ranging from small, discrete middorsal spots to variable semilunar blotches diffusing into paranotal markings and becoming stripes; gonopods with following diagnostic characters: prefemoral process moderately long, uncinate; acropodite thin and fragile, forming completely or nearly complete, broadly symmetrical, loop overhanging and extending well beyond level of prefemoral process; basal zone with inner surface directed mediad; anterior bend and apical curve poorly defined; peak gently curved to flattened, continuous through anterior bend and apical curve with basal and distal zones; latter either coplanar with basal zone or curving through several planes and not coplanar with basal zone, extending downward from peak in medial view then curving into arch and terminating in acute, falcate tip, with or without broadly rounded lobes at midlength; medial flange inconspicuous in medial view.

Remarks. — This species has the largest range in the genus, extending from Canada north of Lake Ontario to southwestern Virginia. There is marked stability in the configuration of the gonopods from central Virginia northward, but in Giles County, the acropodite begins to widen at midlength of the distal zone (base of the upwards curve). South of Giles

County there is a broad lobe at this position whose proximal part is oriented perpendicularly to the medial field of view and whose distal part lies in this plane. Samples from Mountain Lake Biological Station and northern Giles County display intermediate conditions ranging from a slightly wider acropodite at this point to a small rounded lobe. I therefore recognize two subspecies of this assemblage, the oldest available name being *trimaculata* (Wood, 1864), assigned to a population of the northern form from Susquehannah County, Pennsylvania. The oldest available name from the range of the southern race is *kleinpeteri* (Hoffman 1949). Two names were proposed for intergrade forms, *tortua* (Chamberlin 1949) and *picta* (Hoffman 1949), and for the sake of convenience, I place them in synonymy under the nominate subspecies.

Sigmoria (Rudiloria) trimaculata trimaculata (Wood)   Figs. 1-3

Polydesmus (Fontaria) trimaculata Wood, 1864:6; 1865:223-224, Figs. 53-54.
Fontaria lutzi Jacot, 1938:571-572, Fig. 1.
Apheloria trimaculata: Attems, 1938:170. Loomis, 1944:173 (in part). Hoffman, 1949:378.
Apheloria keuka Chamberlin, 1939:10-11, pl. 4, Fig. 32. Chamberlin and Hoffman, 1958:19 **NEW SYNONYMY.**
Apheloria coriacea (nec Koch): Chamberlin, 1947:25, Fig. 5.
Apheloria tortua Chamberlin, 1949:101, Fig. 23. **NEW SYNONYMY.**
Apheloria antrostomicola Hoffman, 1949:372-374, pl. 26, Figs. 1-2. **NEW SYNONYMY.**
Apheloria picta Hoffman, 1949:376-378, pl. 26, Figs. 5-6. **NEW SYNONYMY.**
Apheloria trimaculata trimaculata: Hoffman, 1951:2-3, Fig. 1b. Chamberlin and Hoffman, 1958:20.
Apheloria trimaculata antrostomicola: Hoffman, 1951:3-4, Fig. 1c. Chamberlin and Hoffman, 1958:20-21.
Apheloria trimaculata incarnata Hoffman, 1951:4-5, Fig. 1a. Chamberlin and Hoffman, 1958:21. **NEW SYNONYMY.**
Apheloria trimaculata tortua: Hoffman, 1951:5-6, Fig. 1d. Chamberlin and Hoffman, 1958: 21.
Rudiloria trimaculata: Hoffman, 1978, Figs. 2, 5.
Apheloria (Rudiloria) trimaculata trimaculata: Kevan, 1983:2968.

Type specimens. — Not known to exist; the type locality is in Susquehannah Co., PA (Wood 1864, 1865).

Diagnosis. — Peak relatively flat; distal zone at most only slightly wider at midlength (base of upwards curve), without lobes.

Color in Life. — Variable. Most forms with yellow paranota and concolorous, yellow middorsal spots on caudal edges of otherwise black metaterga, the spots varying in size from small, discrete circles to semilunar blotches spreading laterally along segment margins; some forms with spots connecting by thin line with paranotal markings, others with broad yellow stripes

along caudal edges showing little or no evidence of middorsal spots (see also Hoffman 1949, 1951).

Male from Tucker Co., WV. — Length 33.9 mm, maximum width 7.7 mm, W/L ratio 22.7%, depth/width ratio 59.7%. Segmental widths as follows:

collums 6.4 mm	15th 7.4
2nd-3rd 7.1	16th 7.1
4th 7.4	17th 6.1
5th-14th 7.7	18th 4.9

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.4 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres $2>3>5=6>4>1>7$. Genae without impressions. Facial setae as follows: epicranial 1-1, interantennal absent, frontal 1-1, genal 2-2, clypeal about 10-10, labral about 18-18, merging with clypeal series and continuing for short distance along genal border, about 4 setae per side.

Dorsum smooth, polished, moderately coriaceous on paranota. Collum broad, ends not produced beyond those of following tergite. Paranota moderately depressed, continuing slope of
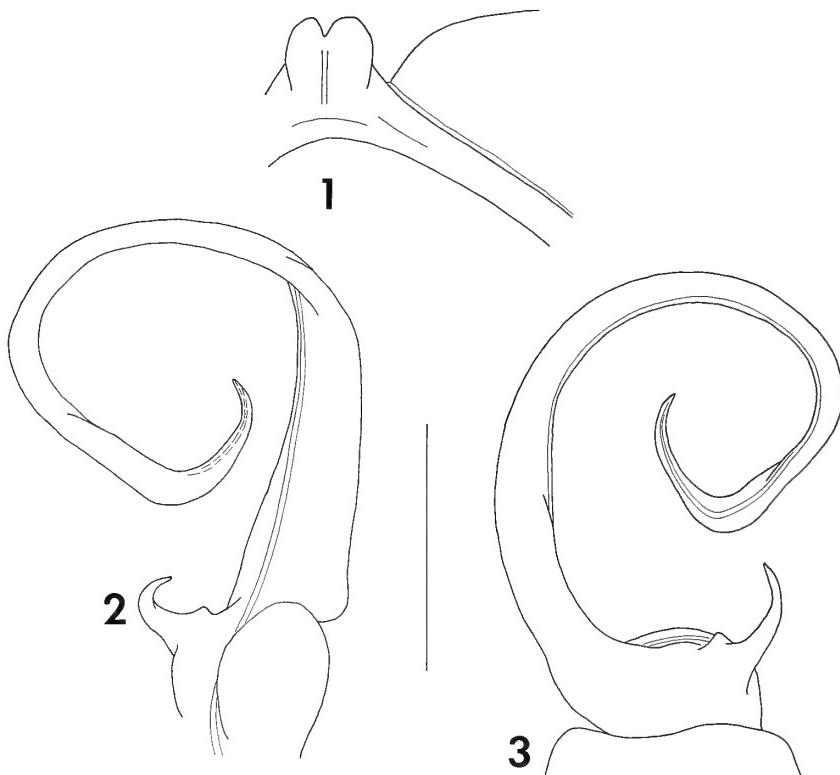
FIGS. 1-3. *Sigmoria (Rudiloria) trimaculata trimaculata.* 1, process of 4th sternum of male from Tucker Co., WV, caudal view. 2, telopodite of left gonopod of the same, medial view. 3, the same, lateral view. Scale line = 1.00 mm for all figures.

dorsum, caudolateral corners rounded through segment 10, becoming blunt and progressively more acute caudally. Peritremata thin but distinct, moderately elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum moderately long, apically divided, length equal to widths of adjacent coxae (Fig. 1); 5th sternum with two low, paramedian knobs between anterior legs and elevated flattened areas between posterior legs; 6th sternum flattened, with very slight convex impression on caudal surface. Postgonopodal sterna flat and plate-like, with bicruciform impressions on segments 8-9 and variably broad, shallow, central impressions on remaining segments. Coxae with low, blunt tubercles beginning on segment 9, becoming longer and sharper caudally; prefemoral spines arising on segment 5, becoming progressively more acute posteriorly.

Gonopodal aperture ovoid, 3.4 mm wide and 1.8 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Hoffman, 1978, Fig. 2) with acropodites curving mediad across midline of aperture, curving dorsad over opposite side then laterad toward midline, overlapping opposite member. Gonopod structure as follows (Figs. 2-3): Prefemoral process moderately long, acute, and falcate, directed mediad, with low, basal spur. Acropodite thin and fragile, in form of flattened loop nearly forming complete circle, overhanging and extending well beyond level of prefemoral process; basal zone relatively long, inner surface directed mediad, sides tapering distad, without modifications; anterior bend moderately broad; peak moderately long, flattened, not continuous with basal zone; apical curve broad, poorly defined; distal zone long, curving broadly downward from peak, linearly into arch, then upwards in a short, linear stretch terminating in acute, falcate tip, sides diverging slightly proximad and broadest at base of upwards curve, tapering smoothly and continuously thereafter; tip directed toward peak in medial view. Medial flange narrow and inconspicuous in medial view, arising on basal zone and blending with medial edge at anterior bend. Lateral flange absent. Prostatic groove crossing to lateral surface at anterior bend, continuing to terminal opening.

Female from Tucker Co. — Length 40.7 mm, maximum width 7.4 mm, W/L ratio 18.2%, depth/width ratio 78.4%. Cyphopods *in situ* with receptacles visible in aperture, valves directed dorsad. Receptacle large, hood-like, enveloping valves, surface rugulose. Valves small, equal, surfaces finely granulate.

Variation. — The gonopods of *trimaculata* are constant throughout the range and do not change with changes in color pattern.

Ecology. — The material I collected in West Virginia and New York was discovered under moist hardwood litter in sheltered sites in deciduous forests.

Distribution. — Northern New England and southern Ontario to west-central Virginia, mostly in upland provinces. This species and *Apheloria corrugata* (Wood), also found in Ontario, are the only two xystodesmids known from eastern Canada, although *Pleuroloma flavipes* Rafinesque may occur in southern Ontario (Shelley 1980b, Kevan 1983). The range of *trimaculata,* around 550 miles long, is the longest documented to date in the Apheloriini. It spans many large rivers, including the St. Lawrence, Connecticut, Hudson, Delaware, Susquehannah, and Potomac. Material was examined as follows:

CANADA. — ONTARIO: *Durham Co.,* Kendal, M, 30 May 1966, and M, 19 July 1967, I.M. Smith (ROM). *Leeds Co.,* Charreys Locks, M, 29, May 1973, J.C.E. Riotte (ROM). *Halton Co.,* Speyside, F, 10 May 1964 (ROM). *Frontenac Co.,* Gull Lake nr. Arden, M, 4 September 1948, R.E. Crabill (NMNH).

UNITED STATES. — MAINE: *Oxford Co.,* Norway, F, date unknown, O. Harger (PMNH).

NEW HAMPSHIRE. — *Sullivan Co.,* Corbin Park, M, date unknown, B.L. Brooks (MCZ). *Rutland Co.,* Tweed River, M, 10 September 1934, collector unknown (UMN). *Bennington Co.,* Beartown, M, 9 June 1954, F.P. Rindge (AMNH).

MASSACHUSETTS. — Berkshire Co., Mt. Greylock, M, 15 June 1936, C.H. Blake (MCZ); and Williamstown, M, 14 June 1936, R. Dow (MCZ).

NEW YORK. — *Steuben Co.,* Lake Keuka, M, September 1905, collector unknown (RVC). *Essex Co.,* Keene Valley, 2M, 22 June and 21 July 1917, H. Notman (AMNH). *Greene Co.,* near Lanesville on NY hwy. 214, 6M, 7F, 18 August 1978 (NCSM A2402). *Ulster Co.,* Phoenicia, M, 25 July 1909, L.J. Barnum (AMNH).

PENNSYLVANIA. — *Potter Co.,* locality unknown, M, F, 3 July 1906, H.W. Fowler (ANSP). *Schuykill Co.,* Tuscarora St. Pk., 5M, 3F, 2 August 1981, H.W. Levi (MCZ).

WEST VIRGINIA. — *Tucker Co.,* along WV hwy. 32, 5.5 mi. E. Lanesville, Monogahela Nat. For., 7M, F, 23 August 1978 (NCSM A2412).

VIRGINIA. — *Highland CO.,* 2 mi. N Williamsville, Bull Pasture R. Gorge, 3M, F, 4 June 1972, R.L. Hoffman (RLH). *Bath Co.,* locality unknown, M, 2F, date and collector unknown (MCZ). *Rockbridge Co.,* Vesovius, F, 11 August 1971, R.H. Perry (RLH). *Alleghany Co.,* 2 mi. NW Clifton Forge, M, 3F, 14 June 1947, R.L. Hoffman (RLH); W side Potts Mtn., 2F, 18 July 1982 R.L. Hoffman (RLH); 8 mi. SW Lowmoor, 16 June 1947, R.L. Hoffman (NMNH).

Remarks. — Because color and color pattern are variable in many eastern xystodesmids, I do not think subspecies should be based solely on these characters. They should be accompanied by corresponding changes in the gonopods as in *latior (Sigmoria).* This was my philosophy with *Pleuroloma* (Shelley 1980b) and races were not recognized in *P. flavipes* Rafinesque. As shown in Table 1, several species of *Sigmoria s. lat.* are polymorphic for color and most have at least an occasional variant, so differences in color or color pattern are not a good basis for taxonomic decisions. The patterns in *t. trimaculata* are also more diverse than previously thought, as a yellow transverse stripe variant occurs in West Virginia.

Additional literature records of *trimaculata* are as follows: Susquehannah Co., PA (Wood 1864, 1865); Keene, Cheshire Co., NH (Jacot 1938); Ithaca, Tompkins Co., NY (Chamberlin, 1939, Loomis 1944); Potter Co., PA, and Garrett Co., MD (Chamberlin 1947); near Staunton and Lyndhurst, Augusta Co., VA (Hoffman 1949); and an unspecified site in Quebec, Canada (Kevan, 1983).

Sigmoria (Rudiloria) trimaculata kleinpeteri (Hoffman), new combination, new status   Figs. 4-7

Apheloria trimaculata (nec Wood): Loomis, 1944:173 (in part).
Apheloria kleinpeteri Hoffman, 1949:375-376, Pl. 26, Figs. 3-4. Chamberlin and Hoffman, 1958:19.

Type specimens. — Male holotype (NMNH) and two male paratypes (RLH) collected by R.L. Hoffman and H.I. Kleinpeter, 30 June 1947, from Burkes Garden, Tazewell Co., Va. Female allotype (NMNH) collected by J.E. Graf, 5 June 1940, at same locality.

Diagnosis. — Peak gently curved; distal zone with broadly rounded lobes at midlength (base of upwards curve), the proximal one perpendicular to field of vision in medial view, the lateral one visible from this respective.

Variation. — The gonopods of *kleinpeteri* are uniform and do not vary appreciably from the condition in the holotype.

Ecology. — Unknown.

Distribution. — Western Virginia and adjacent southern West Virginia. Material was examined as follows:

WEST VIRGINIA. — *Mercer Co.,* Bluefield, East River Mts., M, F, 25 June 1961, R.L. Hoffman (RLH); and along US hwy. 52 above Bluefield, 2M, 20 June 1968, R.L. Hoffman (RLH).

VIRGINIA. — *Giles Co.,* W of Thessalia, near head of Sugar Run, 2M, 3 August 1980, R.L. Hoffman (RLH). *Bland Co.,* 2 mi. S. Long Spur, W side of Little Walker Mtn., F, 16 October 1966, R.L. Hoffman (RLH). *Tazewell Co.,* Burkes Garden, F, 5 June 1940, J.E. Graf (NMNH), M, 30 June 1947, R.L. Hoffman and H.I. Kleinpeter (NMNH), and M, July 1970, collector unknown (RLH). TYPE LOCALITY. *Wythe Co.,* 3 mi. ESE Wytheville, E slope Sand Mtn., F, 1 June 1981, R.L. Hoffman (RLH). *Washington Co.,* along VA hwy. 80 at Hayters Gap, 2M, 8 June 1974, D.W. Ogle (RLH); bluffs on N. Fork Holston R., 4M, 2F, 11 May 1981, D.W. Ogle (RLH); and Brumley Gap, 4M, 24 May 1978, R.L. Hoffman (RLH).

Sigmoria (Rudiloria) trimaculata intergrades

The samples of *trimaculata* from Mountain Lake Biological Station, in northern Giles County, Virginia, display conditions intermediate between those of the two subspecies. They vary from a slightly wider distal zone at midlength to a small rounded lobe at this point, the latter being illustrated by Hoffman (1949, Figs. 5-6). The names *Apheloria tortua* and *A. picta* have been assigned to these forms, and are synonymized with the nominate race. Specimens were examined as follows:

VIRGINIA. — *Giles Co.,* Mountain Lake Biological Station, M, July 1942, A.C. Cole (RVC) and M, F, June 1947, H.H. Hobbs et al. (NMNH).

Sigmoria (Rudiloria) guyandotta (Shear), new combination   Figs. 8-9

Apheloria guyandotta Shear, 1972:494-496, Figs. 1-2.

Type specimens. — Male holotype (MCZ) and six male and two female paratypes (WAS) collected by P. Vogel and M. McGraw, 28 May-1 June 1968, from Shaft Hollow near McGraws, Wyoming Co., WV.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange extending from distal portion of basal zone to midlength of peak and with yellow paranota and red or red-orange middorsal spots, latter tending to
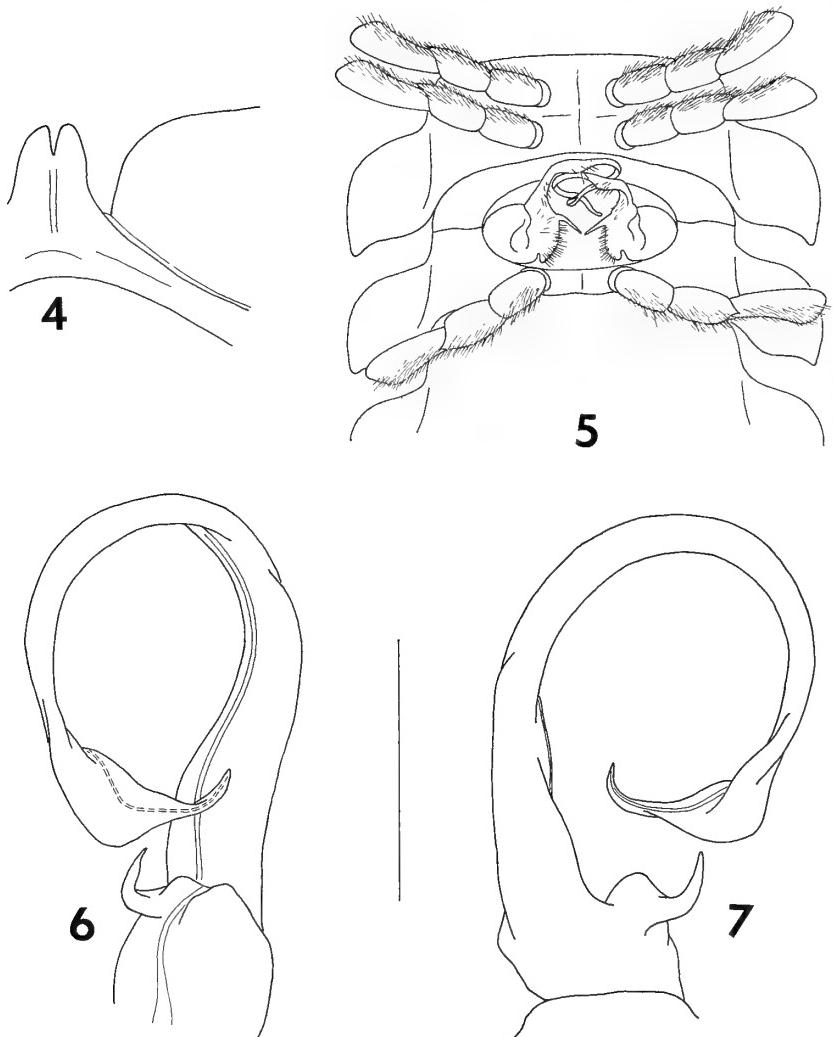
FIGS. 4-7. *Sigmoria (Rudiloria) trimaculata kleinpeteri.* 4, process of 4th sternum of male from Washington Co., VA, caudal view. 5, gonopods *in situ,* ventral view of the same. 6, telopodite of left gonopod of the same, medial view. 7, the same, lateral view. Scale line for fig. 5 = 1.00 mm; line for other figs. = 1.00 mm for each.

form diffuse or distinct metatergal stripes; gonopods with following diagnostic characters: prefemoral process absent; acropodite moderately thick, arch leaning anteriomediad and extending well beyond level of prefemur; basal zone short, inner surface directed mediad; anterior bend poorly defined; peak relatively long, sides narrowing with highest point distad; apical curve well defined; distal zone moderately long, coplanar with basal zone, directed nearly ventrad from peak, flared for entire length with lamellae on both sides, narrowing distad to acuminate tip; medial flange narrow and inconspicuous in medial view; lateral flange narrow and indistinct.

Color in Life. — Variable within species and individuals. According to Shear (1972) the paranota are yellow and the metaterga are black with red or red-orange median spots that may or may not form distinct or diffuse stripes along the caudal edges connecting with the paranotal spots. The collum of the holotype has an anteriomedian red spot with a diffuse yellow stripe along the caudal margin.

Holotype. — The following descriptions of the pregonopodal sterna and the gonopods in "sigmoid" terminology are supplemental to the more complete description by Shear (1972).

4th sternum with small, divided lobe, much shorter than widths of adjacent coxae (Fig. 8); 5th sternum with minute, barely detectable elevations between anterior legs, flat and unmodified between posterior legs; 6th sternum flattened, without depression on caudal edge.

Gonopods *in situ* (see Shear, 1972, Fig. 1) with acropodites extending mediad across midline, lying one in front of other, curving dorsad over opposite side and inserting on opposite prefemur. Gonopod structure as follows (Fig. 9): Prefemoral process absent. Acropodite moderately thick, arch leaning anteriomediad, overhanging and extending well beyond level of prefemur; basal zone relatively short, with inner surface directed mediad; anterior bend moderately broad, poorly defined; peak relatively long, rising continuously to apex at distal extremity, sides narrowing distad; apical curve broad but well defined; distal zone moderately long, coplanar with basal zone, directed nearly ventrad from peak, flared for entire length with lamellae on both sides, narrowing and curving distad to subacuminate tip. Medial flange long and narrow, indistinct, terminating and blending into inner margin of peak distal to midlength. Lateral flange short, narrow, and inconspicuous, located on distal zone opposite ventral bend. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Shear (1972) briefly described somatic features.

Cyphopods *in situ* with receptacles visible in aperture, valves directed dorsad. Receptable large, hood-like, enveloping valves, surface rugulose. Valves small, equal, surfaces finely granulate.

Variation. — The male from Menifee County, Kentucky, has a small, acute, nubbinlike prefemoral process.

Ecology. — Unknown.

Distribution. — Known from two small, allopatric populations in southern West Virginia and east-central Kentucky. Comparatively little sampling has taken place in eastern Kentucky, however, and *guyandotta*

should occur in the intervening area. Material was examined from the following new localities:

KENTUCKY. — *Rowan Co.,* Moreland, M, 14 July 1961, A Razor (FSCA). *Menifee Co.,* 4.5 mi. NE Slade, Dunkan Hollow, M, 3F, 31 August 1957, L. Hubricht (RLH).

Remarks. — Except for being flared, the distal zone of *guyandotta* has the same basic configuration as that of *mohicana,* and the rounded lobe on the outer margin at the apical curve and the beginning of the flare appears homologous to the lobe in that position in *mohicana.* Though more pronounced, the lobes on the distal zone in *t. kleinpeteri,* when examined from the ventral perspective, have a similar configuration to the flange of *guyandotta.* However, the distal zone of *guyandotta* is shorter than that of *t. kleinpeteri,* the flanges are smaller, and the portion distal to the flanges is absent. Thus, the acropodite of *guyandotta* is intermediate between those of *t. kleinpeteri* and *mohicana,* and the forms may be clinally continuous and conspecific. A final decision on their statuses is left to future investigators with access to more material from uncollected areas in Kentucky, West Virginia, and Ohio.

Sigmoria (Rudiloria) mohicana (Causey), new combination   Figs. 10-12

Fontaria trimaculata (nec Wood): Williams and Hefner, 1928:108-109, Fig. 10c.
Rudiloria mohincana Causey, 1955:28-29, Fig. 6.
Rudiloria mohicana: Chamberlin and Hoffman, 1958:47. Hoffman, 1978, Fig. 4.
Apheloria mohicana: Shear, 1972:496-497, Fig. 3.

Type specimens. — Male holotype (AMNH) collected by L. Gray, August 1951, from Mohican State Park, Ashland Co., OH. There are no paratypes.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange extending from distal extremity of basal zone to midlength of peak and with metatergal stripe color pattern; gonopods with following diagnostic characters: prefemoral process absent; acropodite thin and fragile, arch high and rounded, extending beyond level of prefemur; basal zone with inner surface directed mediad; anterior bend poorly defined; peak gently rounded; apical curve with two broad bends; distal zone moderately long, directed laterad from peak, not coplanar with other sections, widest basally with slight proximal lobe on outer margin, tapering to acuminate tip; medial flange narrow and inconspicuous; lateral flange absent.

Color in Life. — Unknown. Causey (1955) described the color pattern after two years in alcohol, and although the pigments had disappeared, the striped pattern was evident. It still is
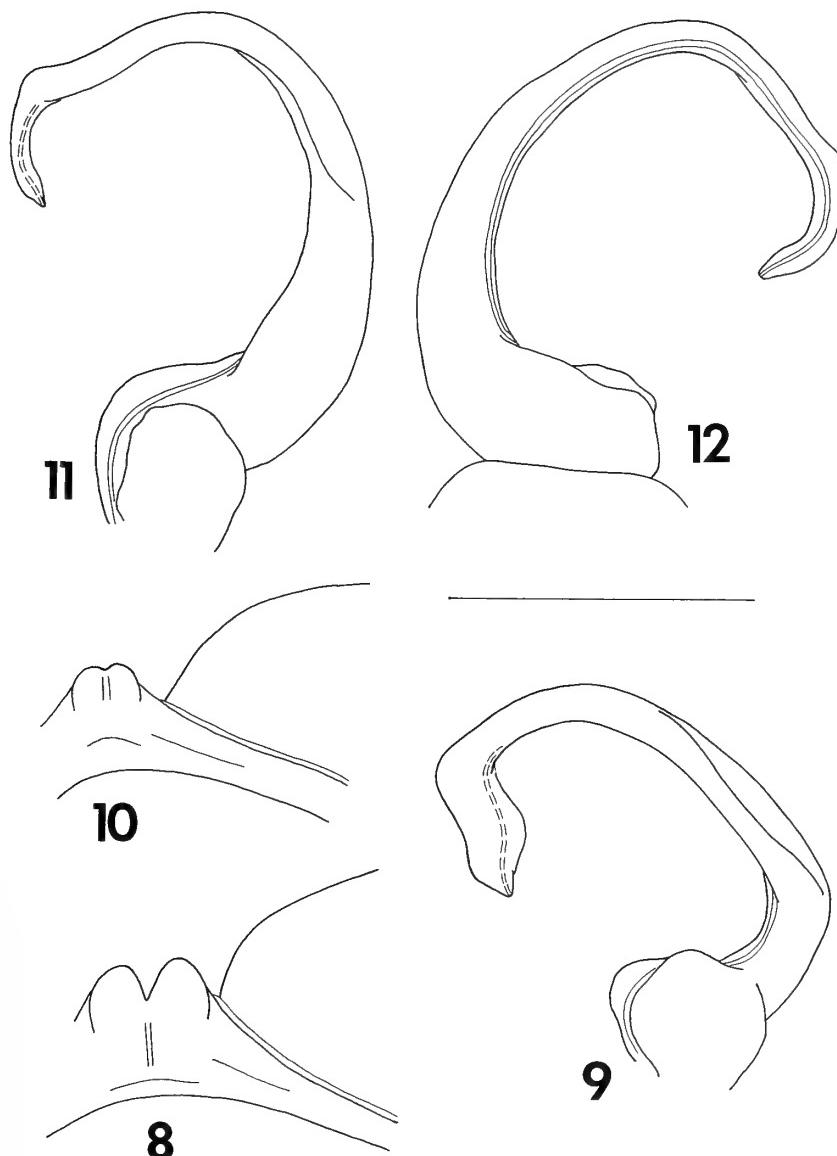
FIGS. 8-12. 8-9, *Sigmoria (Rudiloria) guyandotta*. 8, process of 4th sternum of holotype, caudal view. 9, telopodite of left gonopod of the same, medial view. 10-12, *Sigmoria (Rudiloria) mohicana*. 10, process of 4th sternum of holotype, caudal view. 11, telopodite of left gonopod of holotype, medial view. 12, the same, lateral view. Scale line = 1.00 mm for 10-12; 1.14 mm for 8-9.

today after 30 years of preservation, and there are broad stripes along the caudal margins of the metaterga and both edges of the collum.

Holotype. — The following account of the pregonopodal sterna and the gonopods in "Sigmoid" terminology supplements previous descriptions by Causey (1955) and Shear (1972). 4th sternum with small, undivided lobe, much shorter than widths of adjacent coxae (Fig. 10); 5th sternum with slight elevations between 4th legs and smaller ones between 5th legs; 6th sternum flat, without depression in caudal edge.

In situ arrangement of gonopods unknown. Gonopod structure as follows (Figs. 11-12): prefemoral process absent. Acropodite thin and fragile, forming high arch, gently and unevenly rounded, overhanging and extending beyond level of prefemur; basal zone relatively long, inner surface directed mediad, without modifications; anterior bend broad, poorly defined; peak gently rounded, highest proximal to midlength; apical curve with two broad bends; distal zone moderately long, curving laterad from peak, not coplanar with basal zone, with two bends, widest basally with slight proximal lobe on outer margin, sides narrowing and tapering smoothly to subacuminate tip. Medial flange narrow and inconspicuous, arising near anterior bend, terminating by blending into inner margin of peak near midline, without lobes. Lateral flange absent, possibly represented by slight lobe on outer margin at proximal corner of distal zone. Prostatic groove crossing to lateral surface on basal zone, continuing to terminal opening.

Distribution. — Known from the type locality and probably also Marietta, Washington County, and Athens, Athens County, Ohio (Williams and Hefner 1928).

Remarks. — The acropodite of *mohicana* is convergent with forms of *nigrimontis intermedia (Sigiria)* in its thin, fragile structure, the double bend in the distal zone, and the apical configuration (see Shelley 1981a, Figs. 114-121, p. 114). Also noteworthy is the laterally directed distal zone, which is not coplanar with the basal zone. This feature is less pronounced than that in species of *Falloria* in the Cumberland Plateau of Tennessee, which occur nearly due south of *mohicana*.

Thirty years after its discovery, the type specimen is still the only authentic individual of *mohicana*. Thus, nothing can be said about variation, female anatomy, and ecological preferences since the habitat was not indicated in the original description. This one male is also the only authentic specimen of *Sigmoria s. lat.* from the state of Ohio, which can be expected to have a wealth of forms because the type locality is in the north-central part, about 60 miles south of Lake Erie. I agree with Shear (1972) that *mohicana* probably occurs throughout the hill country of southern Ohio, and one of the remaining needs in the study of *Sigmoria s. lat.* is more material from this state and adjacent parts of West Virginia and Kentucky.

I include under *mohicana* the records of *Fontaria trimaculata* from Athens and Marion, Ohio, published by Williams and Hefner (1928). Their species was probably not *corrugata,* for which they reported a different color pattern and which they claimed was abundant in this section of Ohio.

The gonopod drawings are adjacent, and although from different angles, appear to be of different forms. Hoffman (1951) also reported seeing a new genus and species from Ohio that had been sent to him by Hefner[7] and suggested that it was the same as Williams and Hefner's form. Their drawing of "*trimaculata*" shows a moderately slender, symmetrically curved acropodite with a slightly greater apical curve directed inward into the arch. *Sigmoria (R.) mohicana* appears like this from certain perspectives, and there is a notable similarity between the figure of Williams and Hefner and that of *mohicana* published by Shear (1972, Fig. 3). The absence of a prefemoral process from Williams and Hefner's form also corresponds to the condition in *mohicana*.

Sigmoria (Rudiloria) rigida Shelley, new species   Figs. 13-16

Type specimens. — Male holotype (RLH) and one male and three female paratypes collected by L. Hubricht, 16 June 1956, on Elk River bluffs, 1-1.5 mi. S Clay, Clay Co., WV. One male and three female paratypes (RLH) taken by same collector at same locality, 28 May 1952.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange located on distal portion of basal zone and with metatergal stripe color pattern; gonopods with following diagnostic characters: prefemoral process varying from small nub to small, triangular structure; acropodite thin and fragile, arch flattened and extending beyond level of prefemoral process; basal zone relatively long, inner surface directed mediad; anterior bend well defined; peak long, flattened, edges generally parallel; apical curve with two bends; distal zone moderately long, coplanar with basal zone, linear basally, bending into arch at 2/3 length, widening slightly then narrowing to acuminate tip; medial flange narrow and indistinct in medial view; tooth present at midlength of peak, rigid and spiniform; lateral flange absent.

Color in Life. — Unknown. Preserved material shows a clear pattern of stripes along the caudal margins of the metaterga connecting the paranotal markings and along both the anterior and posterior edges of the collum.

Holotype. — Length 34.5 mm, maximum width 7.9 mm, W/L ratio 22.9%, depth/width ratio 63.3%. Segmental widths as follows:

collum 6.4 mm	16th 7.3
2nd 7.0	17th 6.7
3rd 7.7	18th 5.2
4th-15th 7.9	

---

[7] This sample, from Marietta, Ohio, is present in Dr. Hoffman's collection, but the gonopods are lost and its assignment to *mohicana* needs confirmation.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.3 mm, interantennal isthmus 1.5 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres $2>3>4=5=6>1>7$. Genae without impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 10-10, labral 12-12.
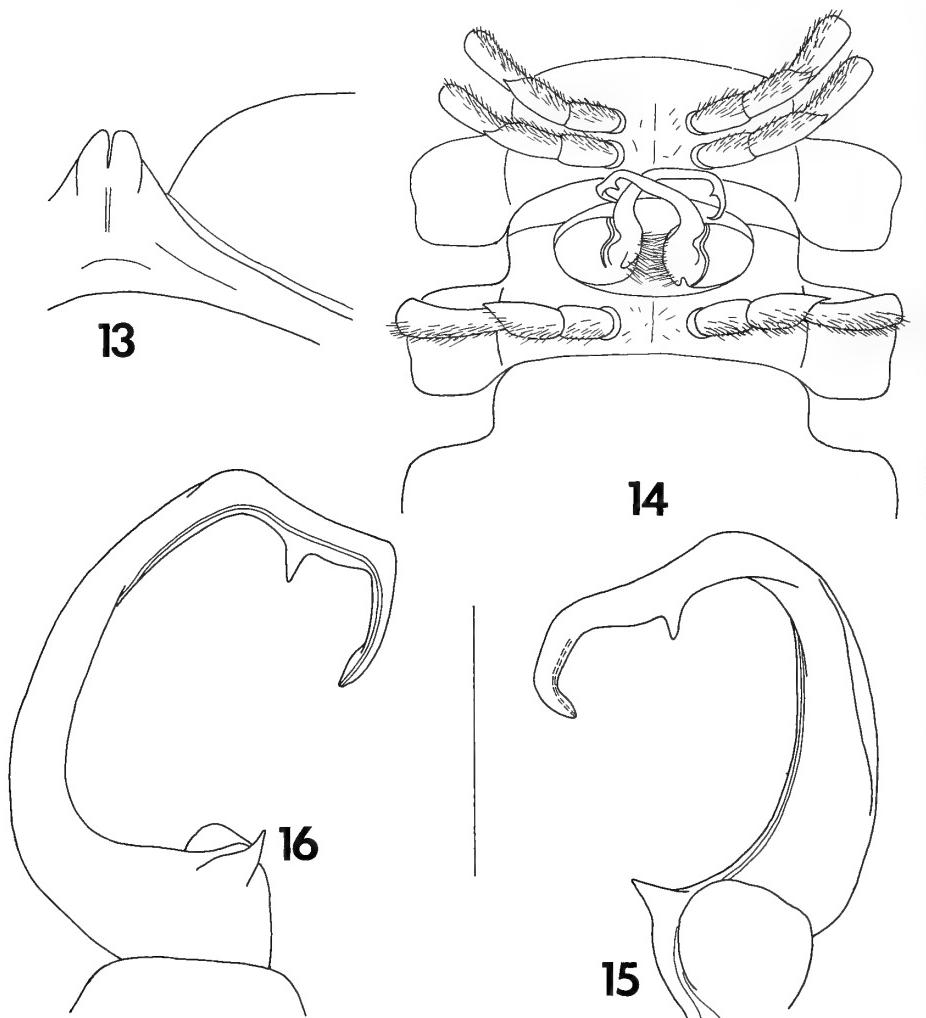
FIGS. 13-16. *Sigmoria (Rudiloria) rigida.* 13, process of 4th sternum of holotype, caudal view. 14, gonopods *in situ,* ventral view of paratype. 15, telopodite of left gonopod of holotype, medial view. 16, the same, lateral view. Scale line for fig. 14 = 1.00 mm; line for other figs. = 1.00 mm for each.

Dorsum smooth, polished, becoming moderately coriaceous on anterior half of paranota. Collum moderately broad, ends broadly rounded and extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 8, blunt on 9-14, becoming progressively more acute posteriorly. Peritremata thin but distinct, moderately elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum apically divided, shorter than widths of adjacent coxae (Fig. 13); 5th sternum with two paramedian knobs between anterior legs, shorter than widths of adjacent coxae, and broad elevated area between caudal legs; 6th sternum flat, without convex recessions in caudal edge. Postgonopodal sterna flat and plate-like, with slight bicruciform impressions on 8 and 9. Coxae with small tubercles beginning on segment 12, becoming progressively larger posteriorly; prefemoral spines arising on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 2.7 mm wide and 1.5 mm long at midpoint, without indentations, sides flush with metazonal surface. Gonopods *in situ* (Fig. 14, of paratype) with acropodites extending mediad across midline, lying one in front of other, curving dorsad over opposite side and touching opposite coxa. Gonopod structure as follows (Figs. 15-16): Prefemoral process small, triangular, directed toward tip of acropodite; prefemur with small, acute spur on medial surface at juncture with basal zone, spur obscured in medial view. Acropodite relatively thin and fragile, forming high, flattened arch, overhanging and extending beyond level of prefemoral process; basal zone relatively long, inner surface directed mediad, without modifications; anterior bend sharp, well defined; peak moderately long, flattened, edges parallel with slight concavity on outer margin; apical curve in two parts, a broad, proximal curve followed by a linear section then a sharp distal curve; distal zone moderately long, coplanar with basal zone, with a linear basal portion bent abruptly into arch at 2/3 length, widening slightly apically then narrowing rapidly to subacuminate tip; latter directed toward prefemur. Medial flange narrow and indistinct, located entirely on basal zone, barely detectable in medial view. Tooth present, a short, rigid spiniform projection at midlength of peak. Lateral flange absent. Prostatic groove crossing to lateral side proximal to anterior bend, continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Badly fragmented and unmeasurable. Cyphopods *in situ* with openings of valves visible in aperture. Receptacle moderate, located anteriomediad to valves, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — Males from Kanawha and Nicholas counties have only a small nubbinlike prefemoral process, and the tooth is slightly shorter and more rounded apically.

Ecology. — Unknown.

Distribution. — Known only from a small triangular area between US highways 19 and 119 in the Elk and Gauley River drainages in central West Virginia. Material was examined as follows:

WEST VIRGINIA. — *Kanawha Co.,* 0.5 mi. N Falling Rock, Elk R. bluffs, M, 28 May 1952, L. Hubricht (RLH). *Clay Co.,* 1-1.4 mi. S Clay, Elk R. bluffs, M, 3F, 28 May 1952, and 2M, 3F, 16 June 1956, L. Hubricht (RLH) and M, F, 7-9 September 1958, MacMillan and Richmond (RLH). TYPE LOCALITY. *Nicholas Co.,* 4 mi NE Swiss, M, 2 September 1965, R.L. Hoffman (RLH).

Remarks. — Similarities between *rigida* and *stenogon/nantahalae (Sigiria/Falloria),* some 240 miles south in southwestern North Carolina are worth noting. The tooth arises suddenly at midlength of the peak, just as in *nantahalae,* and the double bend in the distal zone is similar to that in *stenogon,* although the latter is somewhat bisinuate.

The only differences between *rigida* and *mohicana* are the tooth (present in *rigida,* absent in *mohicana*), the prefemoral process (present in *rigida,* absent in *mohicana*), and a slightly higher and more rounded arch in
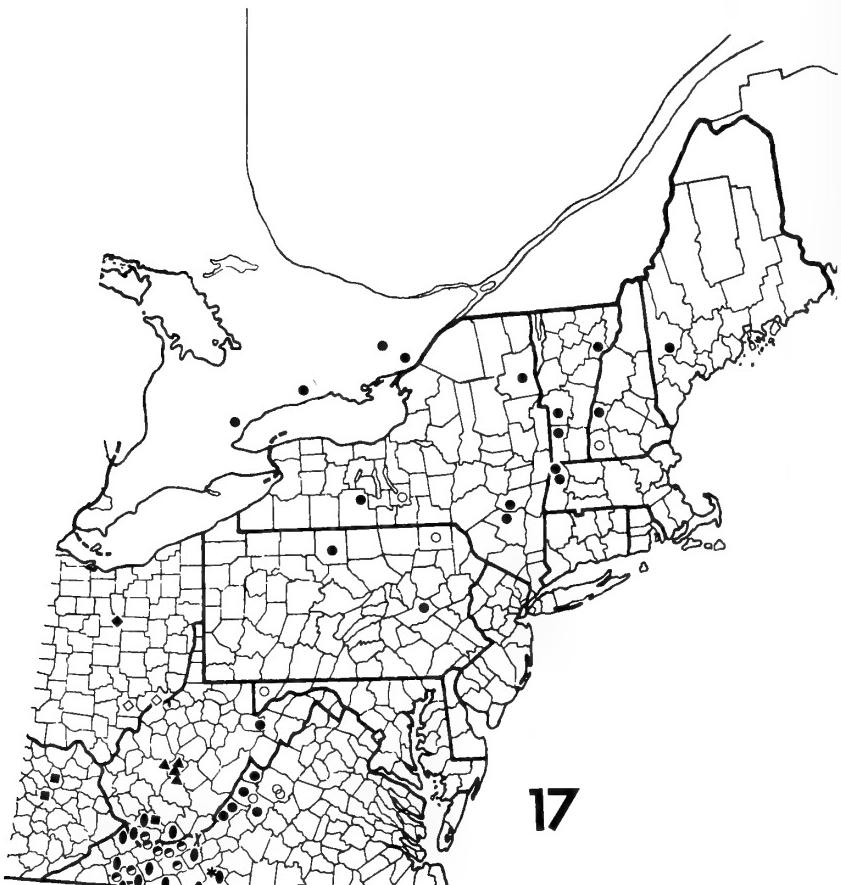
FIG. 17. Distribution of species of *Sigmoria* from Virginia northward, excepting the subgenus *Dixioria.* Ovals, *l. latior;* dots, *t. trimaculata;* half shaded dots, *t. kleinpeteri;* X, *trimaculata* intergrades; squares, *guyandotta;* triangles, *rigida;* diamonds, *mohicana;* asterisk, *whiteheadi.* Open symbols indicate literature records believed to be reliable.

mohicana. The two are thus closely related and may eventually be shown to be subspecies. The hypothesized connection between *t. kleinpeteri, guyandotta,* and *mohicana* may therefore continue eastward and include *rigida*. If so, *Rudiloria* will contain only one species, and the forms will connect in a spiral configuration that curls inward and terminates centrally.

SIGMORIA (DIXIORIA) Chamberlin, new status

Dixioria Chamberlin, 1947:28. Hoffman, 1956a:6-7; 1979:158. Chamberlin and Hoffman, 1958:31. Jeekel, 1971:259.

Type species. — *Dixioria dentifer* Chamberlin, 1947, by original designation.

Diagnosis. — Color pattern constant, paranota yellow, metaterga uniformly black, collum with concolorous yellow stripe along anterior margin; caudolateral corners of paranota rounded through midbody segments; gonopods *in situ* with acropodites extending mostly over opposite side of aperture and inserting beside opposite coxa, perhaps with sides leaning over anterior margin but apices not projecting over latter nor between legs of segment 6; acropodites relatively thin and fragile, without flanges; tooth usually present, located on peak or distal zone; smaller accessory tooth usually present, arising from undersurface of acropodite at or distal to level of tooth; tip simple.

Remarks. — The subgenus *Dixioria* occupies a roughly triangular area in the contiguous corners of North Carolina, Tennessee, and Virginia. The northernmost known locality is in Tazewell County, Virginia, and the Nolichucky River in North Carolina and Tennessee forms a sharp southern distributional limit. The cove dwelling species of the other subgenera do not occur north of this watercourse and are replaced by *Dixioria*. The only sympatric congeners are *latior (Sigmoria)* and *t. kleinpeteri (Rudiloria),* the former being an ecological generalist and thus able to occur outside coves.

The subgenus *Dixioria* is distinguished by both somatic and gonopodal features. The caudolateral corners of the paranota are distinctly rounded over the anterior 2/3 of the body, and even the caudalmost are apically blunt rather than acute. In all other species groups, the caudolateral corners are rounded only through about segments 5-7, after which they become blunt and progressively more acute caudally to around segment 15. Thus, females as well as males can be accurately placed in *Dixioria* on the basis of this diagnostic trait. As in the subgenus *Rudiloria* the gonopods *in situ* extend more mediad than anteriad, projecting over the opposite side of the aperture and often curving dorsad so that the distal zone of one acropodite

touches the coxa of the other. The gonopods are characterized by large prefemoral processes and relatively thin, fragile acropodites. A variable tooth is usually present on the distal extremity of the peak or proximal half of the distal zone, and the forms lacking it have a slightly expanded, rounded medial margin there. Medial and lateral flanges are absent. Six of the seven species display a smaller and sharply acute accessory tooth, which arises from the undersurface of the acropodite at or distal to the level of the main, marginal, tooth. This accessory tooth also is diagnostic for *Dixioria*.

Hoffman (1956a) revised this assemblage, recognizing two species, one with six subspecies. Here I synonymize one subspecies and elevate the others to specific rank. Although the true relationship of *acuminata* to both *pela* and *coronata* in Tennessee remains to be settled, enough collecting has taken place in North Carolina to show that *pela, wrighti,* and *coronata* are not linked by intergrades as in *latior (Sigmoria)*. All have sharp distributional boundaries and are therefore considered reproductively isolated, and a new species exists between *wrighti* and *coronata*. As brief descriptions were previously provided by Hoffman (1949, 1956a), I describe only *pela, brooksi, dactylifera,* and the new species. Supplemental accounts, describing the process of the 4th sternum and the gonopods in "sigmoid" terminology, are provided for the others. *Dixioria* consists of a single species group, the *pela* group.

Components. — *pela* (Chamberlin), *acuminata* (Hoffman), *coronata* (Hoffman), *wrighti* (Hoffman), *watauga* new species, *brooksi* (Hoffman), *dactylifera* (Hoffman).

Sigmoria (Dixioria) pela (Chamberlin), new combination   Figs. 18-24

Fontaria pela Chamberlin, 1918b:122-123. Attems, 1938:167.
Dixioria dentifer Chamberlin, 1947:28-29, Fig. 13.
Dixioria pela pela: Hoffman, 1956a:8-11, Fig. 1a. Chamberlin and Hoffman, 1958:31.
Apheloria pela: Wray, 1950:44; 1967:44.

Type specimens. — Male and female paratypes (RLH, MCZ) collected by R. Thaxter in July of unknown year at Burbank, Carter Co., TN. The holotype is missing from the latter repository where both Hoffman (1956a)

FIGS. 18-24. *Sigmoira (Dixioria) pela.* 18, process of 4th sternum of paratype caudal view. 19, gonopods *in situ,* ventral view of male from Mitchell Co., NC. 20, telopodite of left gonopod of paratype, medial view. 21, the same, lateral view. 22, telopodite of left gonopod of another paratype, medial view. 23, distal zone of male from 3.8 mi. SE Poplar, Mitchell Co., NC, medial view. 24, the same of male from 3.8 mi. SE Spruce Pine, Mitchell Co. Scale line for fig. 49 = 1.00 mm; line for other figs. = 1.00 mm for 23-24, 1.25 mm for 22, 1.43 mm for 18 and 21, and 1.66 mm for 20.
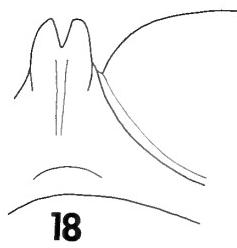
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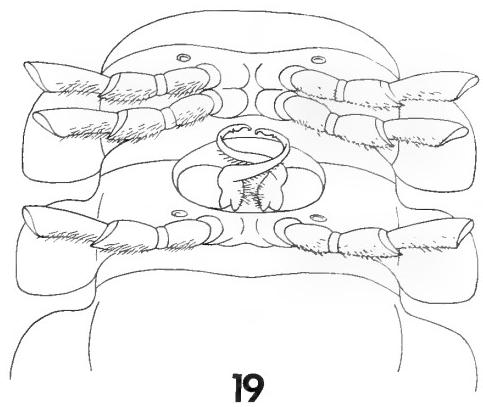
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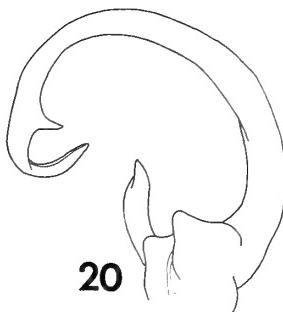
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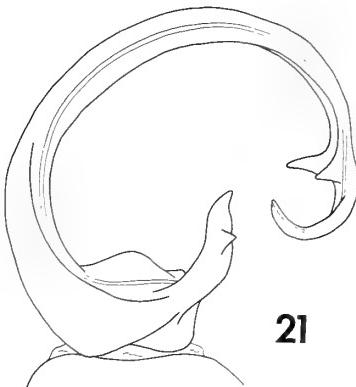
21
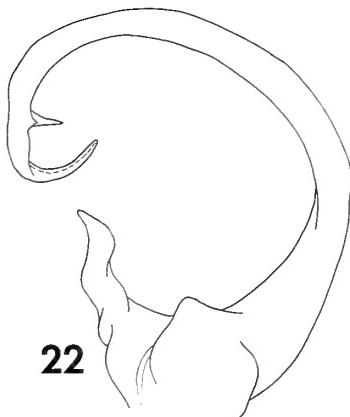
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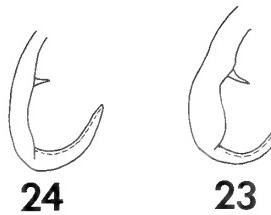
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and Chamberlin and Hoffman (1958) report its deposition. It may be among the Chamberlin material now being accessioned by the NMNH.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, thick, and variably straight, curved, or bisinuate; acropodite thin and fragile, configuration a broad, smooth, continuous curve forming nearly complete circle with prefemoral process; anterior bend and apical curve broad, poorly defined; peak gently curved, apex near midlength; distal zone long, curving broadly dorsad and bending abruptly inward into arch distal to midlength; tooth present or absent, distomedial margin of distal zone slightly expanded and gently rounded when present, not expanded when absent, tooth located proximal to midlength of distal zone, length and configuration variable; accessory tooth present, arising from inner surface of distal zone at level of tooth, variably triangular to spiniform; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Male Paratype. — Length 35.0 mm, maximum width 7.2 mm, W/L ratio 20.6% depth/width ratio 68.0%. Segmental widths as follows:

collum	5.5 mm	14th-15th	7.0
2nd	6.7	16th	6.1
3rd-12th	7.2	17th	5.2
13th	6.8	18th	4.8

Somatic features as in *l. latior,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.6 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>6>4=5>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 8-8, labral about 12-12.

Dorsum finely granulate, becoming smooth and polished on paranota, with very little wrinkling. Collum broad, ends not extending beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 11, blunt on 12-14, becoming progressively more acute posteriorly. Peritremata flat and indistinct, slightly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with moderate process between 3rd legs, length equal to widths of adjacent coxae (Fig. 18); that of segment 5 with two low, medially coalesced knobs between 4th legs, much shorter than widths of adjacent coxae, and rounded, elevated areas between 5th legs; that of segment 6 with convex recession between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on segments 8-10 and variably broad, shallow, central impressions on remaining segments. Coxae with low, blunt tubercles arising on segment 9, becoming progressively longer and sharper caudally; prefemoral spines arising on segment 5, becoming progressively longer and more acute posteriorly.

Gonopodal aperture ovoid, 3.5 mm wide and 1.8 mm long at midpoint, without indentations, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 19, not this specimen)

with acropodites projecting mediad and crossing each other in midline, curving broadly over opposite side of aperture then back toward midline, extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 20-21): prefemoral process a moderately long, upright peg-like projection, directed toward peak and extending beyond level of tip of acropodite, of nearly equal width throughout, narrowing apically, with distal spur on lateral side. Acropodite relatively thin and fragile, configuration a smoothly curved arch overhanging and extending well beyond level of prefemoral process; basal zone moderately long and gently curved, without modifications; anterior bend broad, poorly defined, continuous with apical curve through peak; peak gently curved, apex at midlength; apical curve broad, poorly defined; distal zone long, projecting laterad from peak and not coplanar with basal zone, bending abruptly into arch distal to midlength and tapering to blunt tip; latter directed toward anterior bend. Medial and lateral flanges absent. Tooth moderately long, triangular, and apically subacuminate, located distal to midlength of distal zone; accessory tooth shorter, triangular, and apically acute, located at same position and obscured in medial view. Prostatic groove crossing to lateral side on prefemur and continuing to terminal opening.

Other Male Paratypes. — The type males vary more than those in any other sample. The prefemoral process varies from bisinuate to gently curved, and the arch of the acropodite extends to the level of the prefemoral process in some individuals and well beyond the latter in others. The tooth varies from distinct and sharply triangular to a small, rounded vestige, and the distal zone is slightly wider and has a gently curved medial edge distal to the teeth in the latter condition (Fig. 22).

Female Paratype. — Length 37.6 mm, maximum width 8.7 mm, W/L ratio 23.1%, depth/width ratio 65.5%. Agreeing closely with males in somatic features except coxal tubercles more sharply acute. Cyphopods *in situ* with sides of receptacles visible in aperture, valves directed laterad. Receptacle moderately large, cupped around medial ends of valves, surface rugulose. Valves moderate, equal, surface finely granulate.

Variation. — Variation in the prefemoral process is as described for paratypes, but most individuals resemble the bisinuate condition. On the acropodites the arch is broader in some males, and the great majority lack the tooth. In these the accessory tooth is visible in medial view (figs. 23-24). About half of the available males have an expanded, rounded distomedial margin of the distal zone (Fig. 23), and about half have a narrow, linear edge (Fig. 24). There is no detectable geographic pattern to the distributions of these two forms.

Ecology. — *Sigmoria (D.) pela* is a cove dwelling species. As stated previously by Shelley (1981a), the mountains in northwestern North Carolina north of the Nolichucky-Toe Rivers are more segregated from each other and have fewer ridges and clusters of peaks than those south of this boundary. Consequently, cove environments are rarer, and most forms of *Dixioria* are found along streams under thin layers of leaves on relatively hard substrates.

Distribution. — *Sigmoria (D.) pela* spans the Blue Ridge Province immediately north of the Nolichucky River, from near the escarpment in McDowell-Burke counties, North Carolina, to western Carter County, Tennessee, near the boundary with the Ridge and Valley Province. I have col-

lected extensively south of the Nolichucky and can confirm Hoffman's prediction (1956a) that it forms the southern distributional limit. The range is only two counties wide in each state, and the northern limit does not correspond to any particular physiographic feature. Material was examined as follows:

TENNESSEE. — *Carter Co.,* 1 mi. NW Hampton, Doe River bluff, M, F, 3 May 1951, L. Hubricht (RLH); and Burbank, MM, FF, complete date unknown, R. Thaxter (MCZ, RLH) TYPE LOCALITY. *Unicoi Co.,* 3 mi. E Erwin, co. rd. 2457 at Rock Creek Rec. Area, Cherokee Nat. For., 2M, F, 20 May 1978 (NCSM A1973).

NORTH CAROLINA. — *Avery Co.,* 4.4 mi. N Elk Park, along co. rd. 1305, 1.7 mi. N jct. co. rd. 1307, 2M, 8 September 1973 (NCSM 1999); 2.8 mi. N Elk Park, Elk Falls on co. rd. 1305, M, 29 October 1977 (NCSM A1774); Cranberry, M, 2F, June 1896, A. Wenzell (ANSP); 4 mi. N Newland, along US hwy. 19E, 0.8 mi. S. jct. co. rd. 1168, M, F, 20 June 1980 (NCSM A3323); 6.5 mi. W Newland, along co. rd. 1130, 0.8 mi. W. jct. US hwy. 19E, 3M, 2F, 20 June 1980 (NCSM A3320); and 4 mi. S Newland, along co. rd. 1143, 1.7 mi. NW jct. US hwy. 221, 3M, 20 June 1980 (NCSM A3324). *Mitchell Co.,* 12 mi. NW Bakersville, along co. rd. 1320, 0.7 mi. N jct. co. rd. 1321, 0.8 mi. N jct. co. rd. 1320, 5M, F, 24 July 1975 (NCSM A409); 1.5 mi. N Poplar, along co. rd. 1323, 2.1 mi. N jct. co. rd. 1321, M, 21 May 1978 (NCSM A1976); 11 mi. N Spruce Pine, along NC hwy. 261, 0.1 mi. W jct. co. rd. 1159, M, 21 June 1980 (NCSM A3325); 3 mi. NW Spruce Pine, along co. rd. 1164, 0.5 mi. W jct. co. rd. 1162, 2M, 2F, 21 June 1980 (NCSM A3331); and 3.8 mi. SE Spruce Pine, along co. rd. 1129, 0.4 mi. N jct. co. rd. 1128, 2M, 24 June 1975 (NCSM A408). *McDowell-Burke cos.* — county line on US hwy. 221, 3F, 22 June 1980 (NCSM A3332).

Remarks. — The female only sample from the last locality is tentatively assigned to *pela,* the only proximal species.

The holotype of *D. dentifer,* said by Hoffman (1956a) and Chamberlin and Hoffman (1958) to be at the AMNH, is actually at the ANSP.

Sigmoria (Dixioria) acuminata (Hoffman), new combination, new status

Figs. 25-27

Dixioria pela acuminata Hoffman, 1956a:11-12, Fig. 1b.

Type specimen. — Male holotype (NMNH) collected by J.A. Fowler and R.L. Hoffman, 19 June 1950, from Johnson Co., TN, at the summit of Holston Mountain, 2 mi. W of Shady Valley. There are no paratypes.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, thick, and

FIGS. 25-27. *Sigmoria (Dixioria) acuminata.* 25, gonopods *in situ,* ventral view of holotype. 26, telopodite of left gonopod of holotype, medial view. 27, distal zone of the same, lateral view. Scale line for fig. 25 = 1.00 mm; line for other figs. = 1.00 mm for each.

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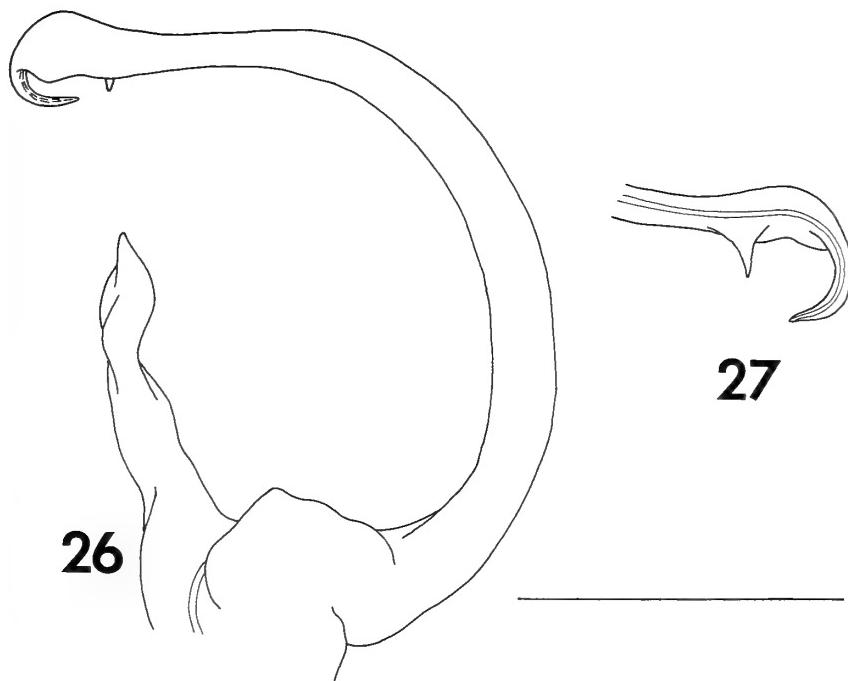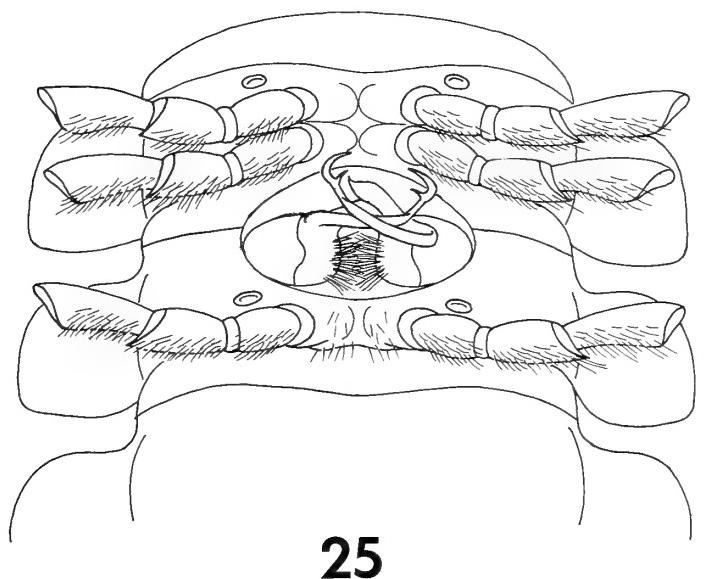
curved; acropodite thin and fragile, configuration a flattened, open arch; anterior bend broad, poorly defined; peak flattened and linear with distal margins slightly expanded and gently rounded; apical curve sharp, well defined; distal zone short, bending sharply into arch, lying parallel to and beneath distal extremity of peak; tooth absent; accessory tooth present, located distad on peak; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae.

Gonopods *in situ* (Fig. 25) with acropodites projecting mediad and crossing each other in midline, curving broadly over opposite side of aperture and extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 26-27): prefemoral process moderately long, upright, indented and curving slightly near midlength, tapering distad to subacuminate tip, directed toward peak. Acropodite relatively thin and fragile, configuration a flattened, open arch extending just beyond level of prefemoral process; basal zone moderately long, gently curved, without modifications; anterior bend broad, poorly defined; peak flattened, linear, distal margins slightly expanded and rounded; apical curve sharp, well defined; distal zone short, not coplanar with basal zone, curving sharply into arch and lying parallel to and beneath distal extremity of peak; tip acuminate. Tooth and medial and lateral flanges absent. Accessory tooth present, arising from inner surface of peak at level of expanded medial margin. Prostatic groove crossing to lateral side on prefemur and continuing to terminal opening.

Variation. — The male from the second locality agrees closely with the holotype.

Distribution. — Known only from Holston Mountain in western Johnson County, Tennessee. The following specimen was examined in addition to the holotype:

TENNESSEE. — *Johnson Co.,* 3 mi. S Shady Valley, along TN hwy. 91, M, 17 May 1964, R.L. Hoffman (RLH).

Remarks. — This is the westernmost form of *Dixioria.* Its true status awaits more sampling in southern Johnson and northern Carter counties, Tennessee, and it might be a subspecies of *pela,* forms of which also lack the tooth and have a slightly expanded distomedial margin of the peak. As Holston Mountain is near the western periphery of the Blue Ridge Province, future investigators should also look for *acuminata* in the adjacent Ridge and Valley Province. Just as *coronata* occurs in this region farther north, *acuminata* may inhabit it on the western side of the subgeneric range.

Sigmoria (Dixioria) coronata (Hoffman), new combination   Figs. 28-31

Deltotaria coronata Hoffman, 1949:380-381, Pl. 26, Figs. 7-8.
Dixioria pela coronata: Hoffman, 1956a:12-13, Fig. 1c. Chamberlin and Hoffman, 1958:31.
Dixioria pela fowleri Hoffman, 1956a:13-14, Fig. 1e. **NEW SYNONYMY.**

Type specimens. — Male holotype, female allotype, and male paratype (NMNH) collected by H.I. Kleinpeter and R.L. Hoffman, 1 July 1947, from Mt. Rogers, Grayson Co., VA.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, variably curved to bisinuate; acropodite moderately thick and heavy, configuration a flattened, open arch; anterior bend broad, poorly defined; peak linear with margins essentially straight; apical curve sharp, well defined; distal zone short, curving gently into arch and nearly overlapping tooth; latter located on distal extremity of peak, apically rounded and moderately long, nearly equal in length to distal zone; accessory tooth present, arising from inner surface of peak beside base of tooth; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae.

Gonopods *in situ* (Fig. 28, ventral view of paratype) with acropodites projecting mediad and crossing each other near midlengths in midline, curving broadly over opposite side of aperture and extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 29-30): prefemoral process relatively long, upright, curving slightly into arch near midlength, apically blunt, directed toward tooth. Acropodite moderately thick and heavy, configuration a flattened, open arch extending to level of prefemoral process; basal zone moderately long, gently curved, without modifications; anterior bend broad, poorly defined; peak flattened and linear, margins straight; apical curve sharp, well defined; distal zone short, curving gently into arch and nearly overlapping tooth, not coplanar with basal zone; tip subacuminate. Medial and lateral flanges absent. Tooth moderately long, apically rounded, located distad on peak; accessory tooth shorter, triangular, and apically acute, located at same position and obscured in medial view. Prostatic groove crossing to lateral side on prefemur, continuing to terminal opening.

Variation. — The distal zone does not curve inward into the arch in northern males (Fig. 31). Otherwise, all gonopods agree closely with those of the holotype.

Ecology. — *Sigmoria (D.) coronata* is a cove dwelling species.

Distribution. — The Watauga River appears to form the southern boundary for this form, which ranges northward into the Ridge and Valley Province to the northern part of southwestern Virginia. It is the only species of *Dixioria* occurring in all three states. Material was examined as follows:

VIRGINIA. — *Tazewell Co.,* Burkes Garden, spring on NE slope of Beartown Mtn., M, 28 August 1977, R.L. Hoffman (RLH). *Bland Co.,* 10 mi. SW Bland, along US hwy. 52 near summit of Big Walker Mtn., 2M, F, 24 June 1950, R.L. Hoffman and J.A. Fowler (NMNH). *Wythe Co.,* Big Walker Mtn., M, 5 May 1955, collector unknown (RLH). *Grayson Co.,* Mt. Rogers, 2M, F, 1 July 1947, R.L. Hoffman and H.I. Kleinpeter (NMNH) and 2M, 24 August

1978, D.W. Ogle (RLH) TYPE LOCALITY; and Comer's Rock Rec. area, 2M, F, 15 June 1950, L. Hubricht (RLH). *Washington Co.,* 4 mi. SW Konnarock, base of Laurel Mtn., 2M, F, 28 April 1951, L. Hubricht (RLH).

TENNESSEE. — *Johnson Co.,* Backbone Rock Rec. Area., Cherokee Nat. For., approx. 4 mi. S Damascus, VA, 2M, F, 11 July 1962, and M, 2 June 1974, R.L. Hoffman (RLH); and along US hwy. 421, 1 mi. W NC state line, several MM, FF, 1 May 1965, collector unknown (RLH).

NORTH CAROLINA. — *Ashe Co.,* 14 mi. NW Jefferson, along co. rd. 1359, 0.5 mi. S. jct. co. rd. 1360, 4M, 3F, 17 June 1980 (NCSM A3295); 12 mi. NW Jefferson, along co. rd. 1356, 0.8 mi. SE jct. co. rd. 1358, 4M, 17 June 1980 (NCSM A3297); 10 mi. NW Jefferson, along co. rd. 1319, 1.7 mi. S jct. co. rd. 1320, M, 21 July 1972 (NCSM 1180); 8.5 mi. SW Jef-
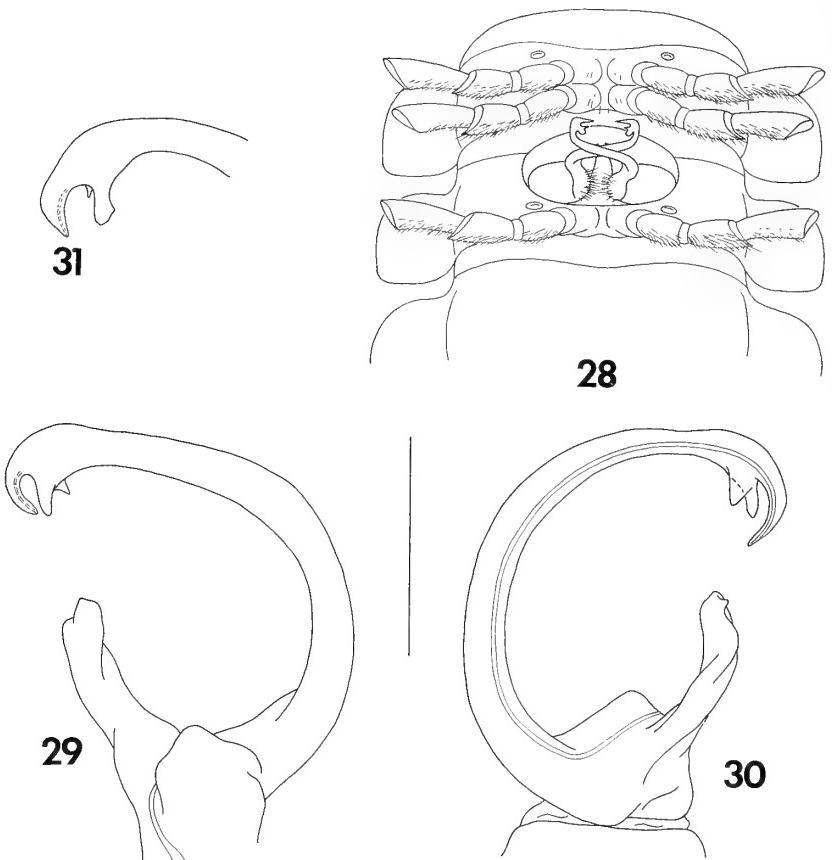
FIGS. 28-31.   *Sigmoria (Dixioria) coronata.*   28, gonopods *in situ,* ventral view of paratype. 29, telopodite of left gonopod of holotype, medial view.   30, the same, lateral view.   31, peak and distal zone of male from Bland Co., VA, medial view. Scale line for fig. 28 = 1.00 mm; line for other figs. = 1.00 mm for each.

ferson, along co. rd. 1100 at Long Hope Cr., 3M, 2F, 17 June 1980 (NCSM A3299); Bina, several MM, FF, 17 May 1964, R.L. Hoffman (RLH); and between Idlewood and Gap Cr., 2M, F, 1 May 1965, collector unknown (RLH). *Watauga Co.,* 3 mi. SE Zionville, headwaters of Meat Camp Cr., M, 3F, 5 September 1971, R.L. Hoffman and L.S. Knight (RLH); 8 mi. NW Boone, along co. rd. 1213, 1.4 mi. SE jct. co. rd. 1201, 4M, 3F, 19 June 1980 (NCSM A3308); and 4 mi. N Vilas, along US hwy. 421, M, 11 June 1962. R.L. Hoffman (RLH).

Remarks. — As shown in figures 29 and 31, the types of *pela fowleri* closely resemble those of *coronata.* The slightly wider gap between the tooth and distal zone could result from a slightly different orientation of the structure for drawing. This is clearly insignificant and *p. fowleri* is placed in synonymy under *coronata,* making it the northernmost representative of *Dixioria.* It occurs sympatrically and perhaps syntopically with *brooksi* at Backbone Rock Recreation Area, Johnson County, Tennessee.

Sigmoria (Dixioria) wrighti (Hoffman), new combination, new status

Figs. 32-34

Dixioria pela wrighti Hoffman, 1956a:15, Fig. 1f.

Type specimens. — Male holotype (NMNH) collected by R.L. Hoffman, 3 August 1949, from Avery Co., NC, approximately 5 mi NE Linville, on the east side of Grandfather Mountain. The female allotype and male paratype, which Hoffman (1956a) reported to be in the NMNH, were not examined.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, curved caudad apically; acropodite thin and fragile, configuration a variably continuous curve directed downward to or below level of prefemoral process, forming complete or nearly complete circle; anterior bend broad, poorly defined; peak variably rounded, apex near midlength; apical curve broad, poorly defined, distal zone long, not coplanar with basal zone, curving broadly dorsad and more abruptly into arch distal to midlength; tooth present near midlength of distal zone, relatively long and nearly overlapping level of tip of acropodite, configuration variably quadriform with sides and distal margin irregular to serrate; accessory tooth arising at level of tooth, triangular to spiniform; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots; collum with broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae.

Gonopods *in situ* (Fig. 32, not this specimen) with acropodites projecting mediad and crossing each other near midlengths in midline, curving broadly over opposite sides of aperture then back toward midline with tips overlapping, curvatures located entirely within aperture. Gonopod structure as follows (Fig. 33-34): prefemoral process relatively long, moderately thick, bent caudad apically, tip subacuminate, directed toward anterior bend. Acropodite relatively thin and fragile, configuration a smoothly continuous curve overhanging and extending well beyond level of prefemoral process, curving downward to or below level of latter forming nearly complete circle; basal zone relatively short, broadly curved; anterior bend broad, poorly defined; peak gently rounded, apex in midlength, sides not expanded; apical curve broad, poorly defined; distal zone moderately long, curving broadly into arch and extending beyond level of tooth, not coplanar with basal zone; tip subacuminate, directed toward anterior bend. Medial and lateral flanges absent. Tooth located near midlength of distal zone, relatively long, sides parallel, with four apical dentations; accessory tooth arising from inner surface of distal zone at same location, shorter and apically acute; partly obscured in medial view. Prostatic groove crossing to lateral side on prefemur, continuing to terminal opening.

Variation. — The degree of jaggedness or serration of the tooth varies on each individual, and there may be from three to five marginal dentations. The acropodite arch is also flattened more in some males, but the distal zone always extends to near the level of the prefemoral process.

Ecology. — *Sigmoria (D.) wrighti* is a cove dwelling species.

Distribution. — A narrow area in the Blue Ridge Province between the Linville and Watauga rivers, extending onto the escarpment in Caldwell County, North Carolina. Specimens were examined as follows:

TENNESSEE. — *Johnson Co.,* along US hwy. 321, 1 mi. W NC state line, 2M, 3F, 1 May 1965, collector unknown (RLH).

NORTH CAROLINA. — *Watauga Co.,* 2 mi. W Sugar Grove, along US hwy. 321, M, 1 May 1965, collector unknown (RLH); 9 mi. W Boone, along co. rd. 1157, 0.1 mi. S jct. co. rd. 1123, 4M, F, 19 June 1980 (NCSM A3314); 7 mi. SW Boone, along NC hwy. 105, 0.8 mi. SW jct. co. rd. 1559, 2M, 19 June 1980 (NCSM A3315); and along US hwy 221 near Caldwell Co. line, M, 31 July 1931, A.W. Petrunkevitch (PMNH). *Avery Co.,* 4.1 mi. S Elk Park, along NC hwy. 194, 3M, 3F, 20 May 1956, R.L. Hoffman (RLH); between Linville and Banner Elk, M, 15 June 1953, R.L. Hoffman (RLH); 13.5 mi. N Newland, jct. US hwy. 321 and co. rd. 1316, M, 19 June 1980 (NCSM A3310); 7 mi. E Newland, along co. rd. 1514, 1 mi. E jct. US hwy. 221, 2M, 20 June 1980 (NCSM A3316); 8 mi. SW Newland, along co. rd. 1530, 0.4 mi. N jct. co. rd. 1511, M, F, 20 June 1980 (NCSM A3318); and 5 mi. NE Linville, along US hwy. 221 on E side Grandfather Mtn., M, 3 August 1949, R.L. Hoffman (NMNH); TYPE LOCALITY. *Caldwell Co.,* Edgemont, 2M, F, 22 June 1980 (NCSM A3333).

Figs. 32-36. 32-34, *Sigmoria (Dixioria) wrighti.* 32, gonopods *in situ,* ventral view of male from Watauga Co., NC. 33, telopodite of left gonopod of holotype, medial view. 34, the same, lateral view. 35-36, *Sigmoria (Dixioria) watauga,* holotype. 35, telopodite of left gonopod, medial view. 36, the same, lateral view. Scale line for fig. 32 = 1.00 mm; line for other figs. = 1.00 mm for each.

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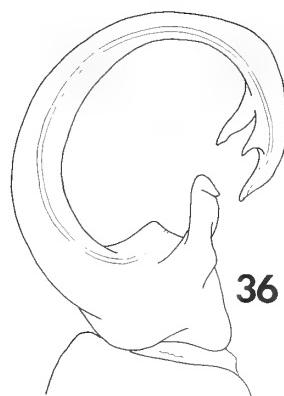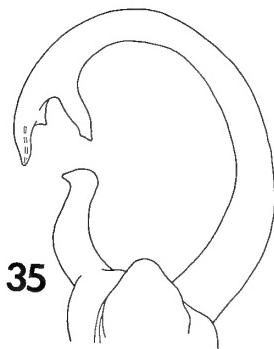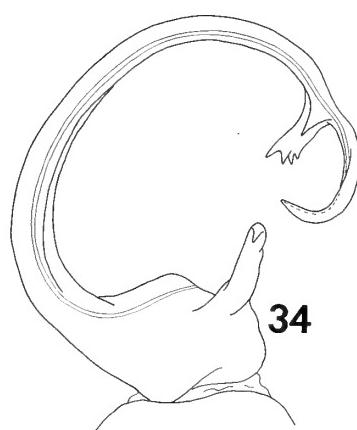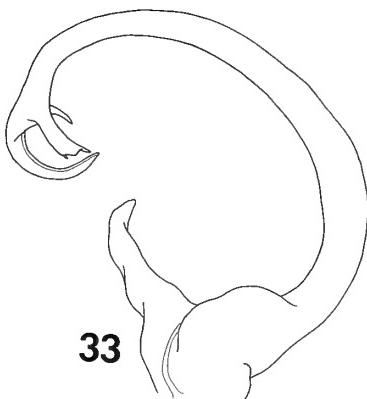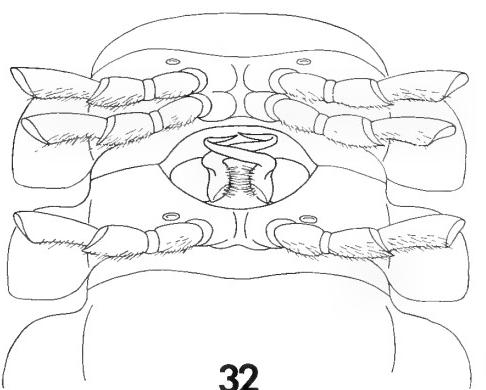
Sigmoria (Dixioria) watauga Shelley, new species   Figs 35-36

Type specimens. — Male holotype (NCSM 2008) and five male and seven
female paratypes collected by R.M. Shelley, 8 September 1973, from yard
of residence on Goforth Rd., 0.5 mi. N US highway 321, Blowing Rock,
Watauga Co., NC. Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange
and with yellow paranota, metaterga without markings; gonopods with
following diagnostic characters: prefemoral process relatively long,
bisinuately curved; acropodite moderately thick and heavy, configuration a
smooth continuous curve extending slightly beyond level of prefemoral
process and directed downward toward latter; anterior bend and apical
curve broad, poorly defined; peak gently curved, apex at midlength; distal
zone moderately long, not coplanar with basal zone, directed downward
toward prefemoral process; tooth present near midlength of distal zone,
relatively long, apically subacuminate and irregular; accessory tooth short
and triangular, arising distal to latter and fully visible in medial view; lateral
flange absent.

Color in Life. — Paranota yellow; metaterga black without stripes or spots, collum with
broad yellow stripe along anterior margin connecting paranotal spots.

Holotype. — Length 38.2 mm, maximum width 8.0 mm, W/L ratio 20.9%, depth/width
ratio 67.5%. Segmental widths as follows:

collum 6.8 mm	15th 7.6
2nd 7.2	16th 6.8
3rd 7.8	17th 6.0
4th-14th 8.0	18th 5.0

Somatic features as in *l. latior,* with following exceptions:

Width across genal apices 3.9 mm, interantennal isthmus 1.6 mm. Antennae reaching back
to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae
with faint central impressions. Facial setae as follows: epicranial and interantennal absent,
frontal 1-1, genal 2-2, clypeal about 10-10, labral about 16-16.

Dorsum smooth, polished, becoming slightly coriaceous on anterior halves of paranota.
Collum broad, ends extending well below those of following tergite. Paranota moderately
depressed, continuing slope of dorsum, caudolateral corners rounded through segment 12,
blunt on segments 13-16. Peritremata distinct, strongly elevated above paranotal surface,
ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with moderate process between 3rd legs, length equal to widths of ad-
jacent coxae; 5th sternum with two low, rounded, medially coalesced knobs between 4th legs
and more separated, equivalent projections between 5th legs; 6th sternum convexly recessed
between 7th legs to accommodate apical curves of acropodites, 7th legs set slightly farther
apart than 6th. Postgonopodal sterna generally flat, with variably broad, shallow, central im-
pressions. Coxae with low, rounded tubercles beginning on segment 16; prefemoral spines
beginning on segment 6, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 3.9 mm wide and 1.4 mm long at midpoint, without indenta-
tions, sides elevated above metazonal surface. Gonopods *in situ* with acropodites projecting
mediad and crossing in midline, curving broadly over opposite side of aperture and extending

dorsad, lying entirely over aperture. Gonopod structure as follows (Figs. 35-36): prefemoral process relatively long, bisinuate, apically subacuminate. Acropodite moderately thick and heavy, configuraton a smooth, continuous curve extending slightly beyond level of prefemoral process and curving downward in medial view (dorsad); basal zone moderately long, gently curved; anterior bend broad, poorly defined, continuous through peak with apical curve; peak relatively short, gently curved, apex at midlength; apical curve broad, poorly defined; distal zone moderately long, curving slightly laterad from peak and not coplanar with basal zone, projecting downward in medial and lateral views and extending to level of prefemoral process; tip subacuminate, directed toward coxa. Medial and lateral flanges absent. Tooth moderately long, apically subacuminate and irregular, located near midlength of distal zone; accessory tooth short and acute, arising distal to tooth and fully visible in medial view. Prostatic groove crossing to lateral side on prefemur and continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 39.4 mm, maximum width 8.4 mm, W/L ratio 21.3%, depth/width ratio 69.0%. Cyphopods *in situ* with openings of valves and corners of receptacles visible in aperture. Receptacle moderate, cupped around lateral sides of valves, surface rugulose. Valves small, equal, surfaces finely granulate.

Variation. — The gonopods are all quite similar. The tooth is slightly longer in western populations, and the midlength bend of the prefemoral process is considerably broader in that from Wilkes County.

Ecology. — *Sigmoria (D.) watauga* is primarily a cove species, although it can occur away from water sources. The type specimens were found under ivy, in moist litter, in corners of walkways, and in the basement of the residence at Blowing Rock.

Distribution. — A triangular area in the Blue Ridge Province of North Carolina, mostly in Watauga County. The species is common in the communities of Boone and Blowing Rock. Specimens were examined as follows:

NORTH CAROLINA. — *Watauga Co.,* 12 mi, WNW Boone, along US hwy. 321, 1.5 mi. N Avery Co. line, 2M, 129 June 1980 (NCSM A3309); Boone, Appalachian State Univ. campus, 2M, 3F, 26 April 1974 (NCSM 2212); 1.9 mi. S Boone, along co. rd. 1549, 0.7 mi. jct. co. rd. 1550, 4M, 26 April 1984 (NCSM 2216); 6.2 mi. E Boone, along co. rd. 1508, 1.2 mi. S jct. Blue Ridge Pkwy., 4M, 3F, 18 June 1980 (NCSM A3303); 2.2 mi. N Blowing Rock, along co. rd. 1541, 1.5 mi. N jct. co. rd. 1552, 2M, 26 April 1974 (NCSM 2221); and Blowing Rock, residence on Goforth Rd., 0.5 mi. N jct. US hwy. 321, 6M, 7F, 8 September 1973 (NCSM 2008) TYPE LOCALITY. *Wilkes Co.,* 18.1 mi. WNW Wilkesboro, Jeffress Pk. Recreation area on Blue Ridge Pkwy., 4M, 2F, 18 June 1980 (NCSM A3302).

Remarks. — The male from Boone that Hoffman (1956a) considered an intergrade between *pela wrighti* and *p. coronata* is referable to *watauga*.

Sigmoria (Dixioria) brooksi (Hoffman), new combination   Figs. 37-40

Dixioria pela brooksi Hoffman, 1956a:12, Fig. 1d.
Dixioria brooksi Hoffman, 1969:227.

Type specimens. — Male holotype and male paratype (NMNH) collected by Dr. and Mrs. S.T. Brooks, 14 August 1941, on Holston Mountain near Damascus, Washington Co., VA. Hoffman (1956a) stated that male and female topoparatypes were deposited in the Carnegie Museum, Pittsburgh, PA, but I did not find them in a visit there in 1978.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process long, thick, and linear, tapering distad to acuminate tip; acropodite moderately thick and heavy, configuration an upright, open arch with apex overhanging level of pre-femoral process; anterior bend sharp, well defined; peak moderately long and straight, outer margin expanded distad into broadly rounded lobe forming apex of arch; distal zone short, terminating well above prefemoral process, directed laterad from peak and not coplanar with basal zone, sides tapering to acuminate tip directed toward basal zone; medial and lateral flanges absent; tooth present on distal extremity of peak, short and truncate, extending to same level as tip of distal zone, distal margin linear, angling to lower inner corner; accessory tooth present, short and acute, arising from base of tooth, obscured by latter in medial view.

Color in Life. — Unknown. Hoffman (1956a) did not report this, and there is no fresh material. However, faded markings on the preserved specimens indicate the coloration of other members of *Dixioria.*

Holotype. — Length 35.2 mm, maximum width 7.6 mm, W/L ratio 21.6%, depth/width ratio 60.5%. Segmental widths as follows:

collum 5.4 mm	13th-15th 7.0
2nd 6.9	16th 6.8
3rd 7.2	17th 6.1
4th-12th 7.6	18th 4.9

Somatic features similar to those of *l. latior,* with following exceptions:

Width across genal apices 3.9 mm, interantennal isthmus 1.4 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres $2 > 3 > 4 = 5 = 6 > 1 > 7$. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 12-12, labral about 18-18.

Dorsum smooth, polished, slightly coriaceous on anterior halves of paranota. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 13, blunt on 13-15, acute on remaining segments. Peritremata moderately distinct, slightly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with moderate process between 3rd legs, length equal to widths of adjacent coxae (Figs. 37); that of segment 5 with slight medial process between 4th legs, much shorter than widths of adjacent coxae, and low, rounded, elevated areas between 5th legs; that of segment 6 with moderate, convex recession between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on segments 8-10, flattened and plate-like thereafter. Coxae with low,

blunt tubercles arising on segment 13; prefemoral spines arising on segment 8, becoming pro-
gressively longer and sharper caudally.

Gonopodal aperture ovoid, 3.2 mm wide and 1.9 mm long at midpoint, indented slightly
anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 38, not this
specimen) with acropodites angling mediad and apices lying over and under each other in
midline, extending forward slightly beyond anterior margin. Gonopod structure as follows
(Figs. 39-40): prefemoral process relatively long, linear, tapering distad to acuminate tip,
directed toward distal zone. Acropodite moderately thick and heavy, well sclerotized, arch
upright, bent abruptly at 2/3 length and extending to but not beyond level of prefemoral
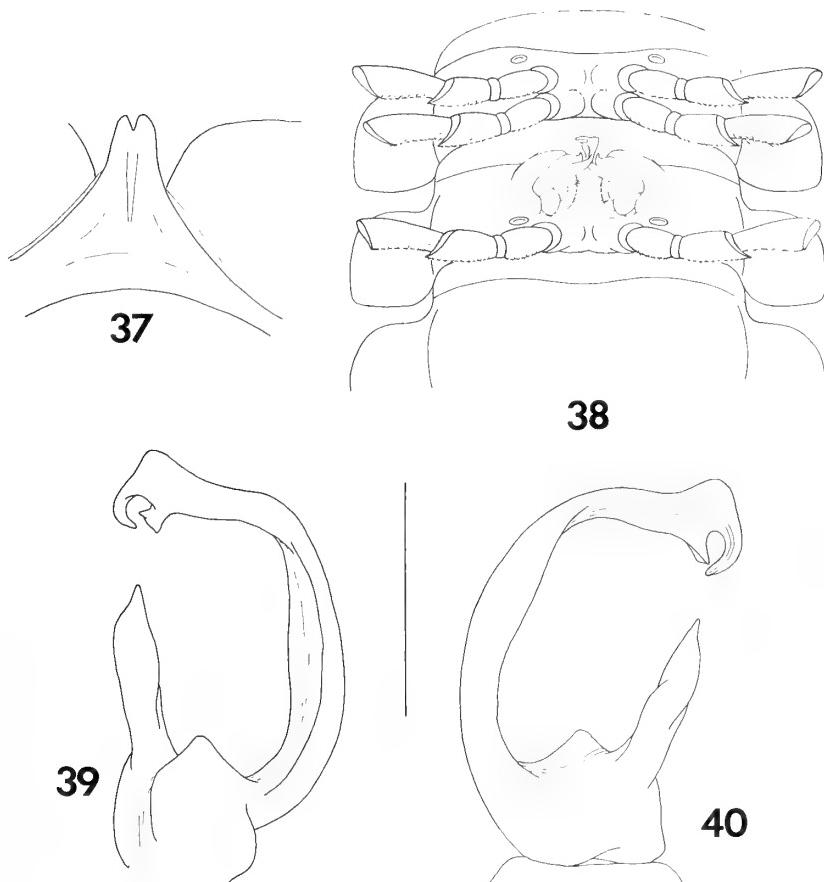
Figs. 37-40.   *Sigmoria (Dixioria) brooksi.*   37, process of 4th sternum of holotype, caudal
view. 38, gonopods *in situ,* ventral view of male from Johnson Co., TN. 39, telopodite of
left gonopod of holotype, medial view. 40, the same, lateral view. Scale line for fig. 38 = 1.00
mm; line for other figs. = 1.00 mm for 37, 1.23 mm for 39-40.

process; basal zone relatively long, nearly straight; anterior bend sharp, well defined; peak moderately long and linear, outer margin expanded distad into rounded lobe forming highest point on acropodite arch; apical curve sharp, well defined; distal zone short, angling slightly laterad from peak, not coplanar with basal zone, directed downward toward prefemur then bending into arch, nearly overlapping tooth; tip subacuminate, directed toward basal zone. Medial and lateral flanges absent. Tooth short, apically broad and truncate, outer corner slightly produced, located at distal extremity of peak; accessory tooth equal in length to, and arising from base of, tooth, obscured in medial view, apically acuminate. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Male Paratype. — The male paratype agrees with the holotype in all particulars.

Female Paratype. — As the specimen supposedly at the Carnegie Museum could not be located, the female characters of *brooksi* are unknown.

Variation. — The male from Tennessee agrees closely with the holotype.

Distribution. — Known from the type locality and the following site, which is only about four miles southeast.

Remarks. — Although *brooksi* possesses an accessory tooth and resembles *coronata* in the general form of the acropodite and the short distal zone that curves inward, nearly overlapping the tooth, it is not conspecific. The two occur sympatrically at Backbone Rock Recreation Area and hence are reproductively isolated. The male of *brooksi* was even discovered in a vial with one of *coronata,* suggesting that they are syntopic. The course of the prostatic groove differs, as it crosses to the lateral surface at the anterior bend in *brooksi* and on the prefemur in *coronata.* Likewise, they are distinguished by the configuration of the peak, which is expanded into a distolateral lobe in *brooksi* and is nearly linear in *coronata.* The lobe in *brooksi* culminates the tendency toward enlargement at this position found in *dactylifera* and *acuminata.* It is similar in appearance to, and apparently convergent with, that of *translineata (Falloria)* (compare Figs. 39-40 with Figs. 68-69 in Shelley (1981a)).

TENNESSEE. — *Johnson Co.,* Backbone Rock Recreation Area, Cherokee National Forest, along TN hwy. 41 about 4 mi. S of Damascus, VA and the state line, M, 2 June 1974, R.L. Hoffman and L.S. Knight (RLH).

Remarks. — Although *brooksi* possesses an accessory tooth and resembles *coronata* in the general form of the acropodite and the short distal zone that curves inward, nearly overlapping the tooth, it is not conspecific. The two occur sympatrically at Backbone Rock Recreation Area and hence are reproductively isolated. The male of *brooksi* was even discovered in a vial with one of *coronata,* suggesting that they are syntopic. The course of the prostatic groove differs, as it crosses to the lateral surface at the anterior bend in *brooksi* and on the prefemur in *coronata.* Likewise, they are distinguished by the configuration of the peak, which is expanded into a distolateral lobe in *brooksi* and is nearly linear in *coronata.* The lobe

in *brooksi* culminates the tendency toward enlargement at this position found in *dactylifera* and *acuminata*. It is similar in appearance to, and apparently convergent with, that of *translineata (Falloria)* (compare Figs. 39-40 with Figs. 68-69 in Shelley (1981a)).

Sigmoria (Dixioria) dactylifera (Hoffman), new combination   Figs. 41-44

Dixioria dactylifera Hoffman, 1956a:15-16,Fig. 2.

Type specimens. — Male and female paratypes (AMNH, NMNH) collected by C.M. and R.D. Breeder, 22 August 1910, at Mill Hill (precise location unknown), Ashe Co., NC. The male holotype said by Hoffman (1956a) to be deposited in the AMNH is not there and apparently is lost.

Diagnosis. — A moderate-size species of *Sigmoria* without medial flange and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process moderately long and gently curved ventrad, apically subacuminate; acropodite moderately thick and heavy, configuration an open arch leaning over and extending slightly beyond level of prefemoral process; anterior bend broad, poorly defined; peak relatively long, margins essentially straight; apical curve sharp, well defined; distal zone short, terminating well above level of prefemoral process, directed laterad from peak and not coplanar with basal zone, sides tapering to acuminate tip directed parallel to prefemoral process; medial and lateral flanges absent; tooth present on distal extremity of peak, relatively long, extending below level of distal zone, sides parallel, distal margin linear, inner apical corner produced to form subacuminate tip projecting inward into arch and directed toward basal zone; accessory tooth absent.

Color in Life. — Paranota bright lemon yellow; metaterga dark glossy black without stripes or spots; collum with narrow yellow stripe along anterior margin connecting paranotal markings.

Male Paratype. — Length 56.9 mm, maximum width 7.4 mm, W/L ratio 20.1%, depth/width ratio 60.8%. Segmental widths as follows:

collum 5.9 mm	15th 7.2
2nd 6.5	16th 6.8
3rd 7.0	17th 5.8
4th-14th 7.4	18th 4.2

Somatic features similar to those of *l. latior,* with following exceptions:

Width across genal apices 3.9 mm, interantennal isthmus 1.7 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>5>6>4>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 9-9, labral about 12-12, merging with clypeal series and continuing for short distance along genal borders, about 3 setae per side.

Dorsum smooth, polished, slightly coriaceous on anterior halves of paranota and extending mediad along margins of strictures. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 13, blunt on 14-16, acute on remaining segments. Peritremata moderately thick and distinct, well elevated above paranotal surfaces, ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with small process between 3rd legs, shorter than widths of adjacent coxae (Fig. 41); that of segment 5 with low projection between 4th legs, much shorter than
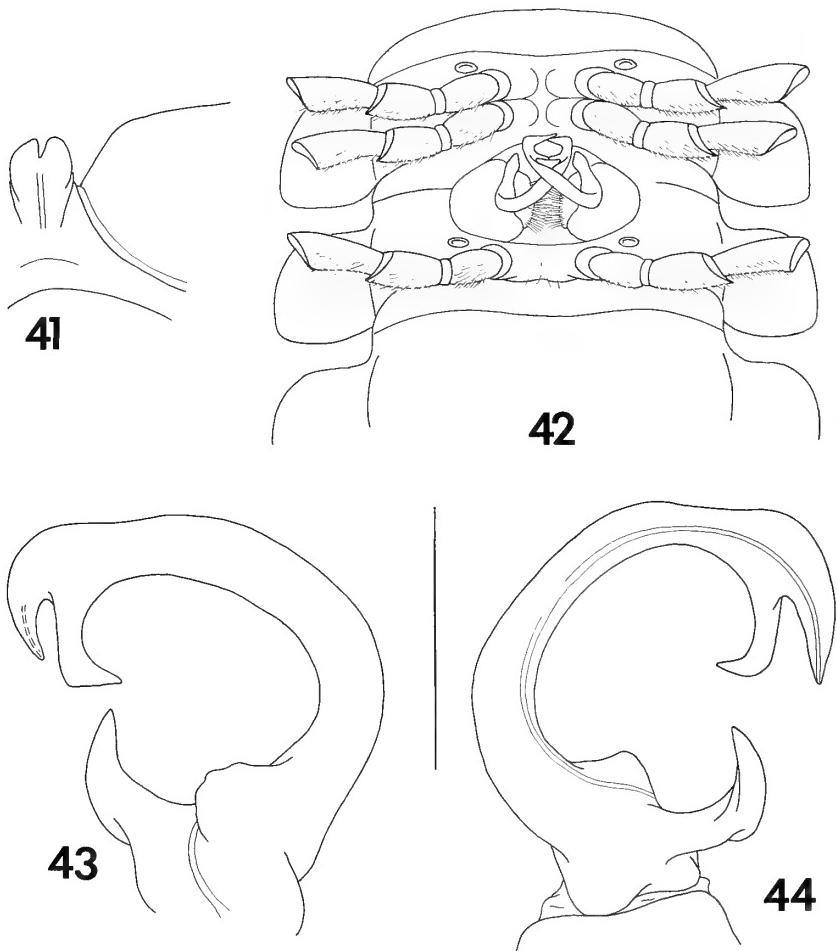
FIGS. 41-44. *Sigmoria (Dixioria) dactylifera.* 41, process of 4th sternum of paratype, caudal view. 42, gonopods *in situ,* ventral view of male from Mt. Jefferson St. Pk., Ashe Co., NC. 43, telopodite of left gonopod of paratype, medial view. 44, the same, lateral view. Scale line for fig. 42 = 1.00 mm; line for other figs. = 1.00 mm for each.

widths of adjacent coxae, and higher, flattened, elevated areas between 5th legs; that of segment 6 with deep, convex depression between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on segments 8-11, with variably broad, shallow, central depressions on remaining segments. Coxae with low blunt tubercles arising on caudal legs of segment 13; prefemoral spines arising on segment 6, becoming longer and sharper caudally.
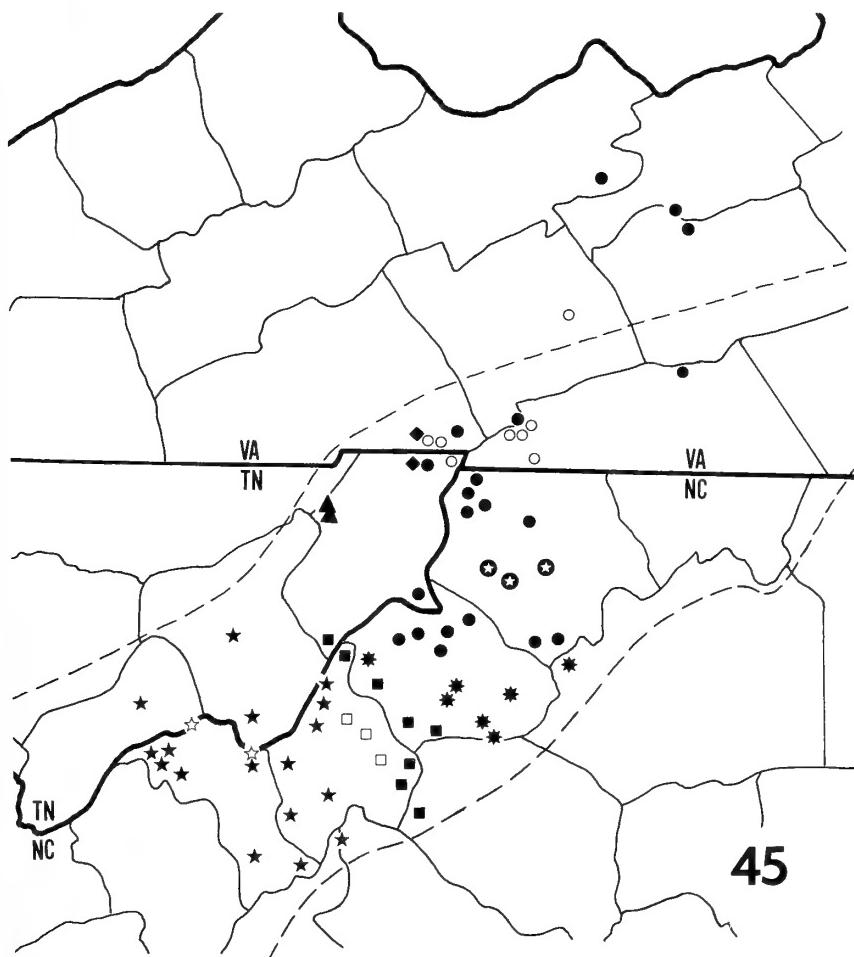
FIG. 45.   Distribution of the subgenus *Dixioria* in North Carolina, Tennessee, and Virginia. Stars, *pela;* triangles, *acuminata;* dots, *coronata;* squares, *wrighti;* asterisks, *watauga;* diamonds, *brooksi,* stars in dots, *dactylifera.* Open symbols represent unconfirmed records from Hoffman (1956a) that are believed to be correct. The dashed lines show the approximate boundaries of the Blue Ridge Province.

Gonopodal aperture ovoid, 3.3 mm wide and 1.8 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 42, not this specimen) with acropodites crossing in midline of aperture, curving slightly over opposite side then back toward midline with apices overlapping, extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 43-44): Prefemoral process moderately long, thick, and heavy, curving broadly ventrad and directed toward tooth, tip subacuminate. Acropodite moderately thick and heavy, arch broadly curved, leaning over and extending slightly beyond level of prefemoral process; basal zone short, broadly curved; anterior bend broad, poorly defined; peak relatively long and straight, apex near midlength; apical curve sharp, well defined; distal zone short, curving strongly laterad from peak and not coplanar with basal zone, directed downward from peak in medial view with only very slight curve; tip acuminate, directed parallel to prefemoral process. Medial and lateral flanges absent. Tooth long, extending below level of distal zone, directed linearly from distal extremity of peak with sides parallel, inner apical corner produced to form acuminate tip projecting inward into arch and directed toward basal zone; accessory tooth absent. Prostatic groove crossing to lateral side on prefemur, continuing on this surface to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype.

Female Paratype. — Length 37.2 mm, maximum width 7.9 mm, W/L ratio 21.2%, depth/width ratio 64.6%. Cyphopods *in situ* with receptacle visible in aperture, valves directed laterad. Receptacle large, hood-like, enveloping medial and ventral surfaces of valves, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — All males of *dactylifera* are nearly identical to each other.

Ecology. — The male I collected in Mt. Jefferson State Park was discovered at the picnic area near the summit under moist litter in a deciduous forest. The site lacked rhododendron and a water source, and could not be classified as a cove.

Distribution. — Known only from three localities in the northwestern corner of North Carolina. Material was examined as follows:

NORTH CAROLINA. — *Ashe Co.,* Mill Hill, exact location unknown, 6M, 5F, 22 August 1910, C.M. and R.D. Breeder (AMNH, NMNH) TYPE LOCALITY; 2 mi. SE Creston, Three-Top Mtn., 4M, 4F, 23 July 1963, R.L. Hoffman (RLH); and Mt. Jefferson St. Pk., M, 29 August 1976 (NCSM A1412).

Remarks. — The principle diagnostic features of *dactylifera* are the distinctive configuration of the tooth and the absence of the accessory tooth.

SIGMORIA (SIGMORIA) Chamberlin, new status

Sigmoria Chamberlin, 1939:7. Hoffman, 1950:1-2; 1979:158. Chamberlin and Hoffman, 1958:49. Jeekel, 1971:287. Shelley, 1981a:16-18.

Type species. — *Sigmoria munda* Chamberlin, 1939, by original designation.

Diagnosis. — Paranota yellow to red, metatergal color pattern variable, either uniformly black or with concolorous stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture and inserting between 7th legs; acropodites moderately thick, oriented normally on coxa with inner surface directed anteriomediad; basal zone without modifications; with variable laminate medial flange located on peak; with or without variable lateral flange and variable tooth on peak distal to flange; tip either reflexed or with this configuration.

Remarks. — The nominate subgenus occupies a broad area from southern West Virginia to the Savannah River and the Atlantic Ocean. In the north it overlaps all of *Dixioria* and the southern extremity of *Rudiloria,* and in the south it overlaps the South Carolina forms of *Cleptoria* and all species of *Croatania* except *yemassee.* Although less common in the mountains, it ranges westward into the central Blue Ridge Province and overlaps parts of *Sigiria* and *Cheiropus.* Most of its range is due to the widespread, ubiquitous *latior,* a clinally continuous species composed of three geographic races connected through a broad area of intergrades (Shelley 1976, 1981a). In the western Piedmont of North Carolina occurs a second species, *stenoloba,* that apparently arose from *latior* by ecological isolation and is comprised of two allopatric populations. Two additional, localized species occur in the eastern Piedmont and Fall Zone of southern South Carolina. They are sufficiently different from *latior* and *stenoloba* that I divide *Sigmoria s. str.* into two species groups.

The *Latior* Group

In the *latior* group, the acropodites are moderately thick and heavy, the anterior bend and apical curve are sharp and well defined, and the peak is flattened and constitutes about 1/3 of the total length. The medial flange is variably broad, located on the proximal part of the peak, and clearly demarcated from the acropodite stem. The distal zone terminates in a reflexed tip; has a long, narrow flange; and usually exhibits a tooth distal to the medial flange. The *latior* group overlaps partly the *quadrata* group, and its range is essentially that of the subgenus.

Components. — *latior* (Brolemann) [*l. latior, l. munda* Chamberlin, *l. hoffmani* Shelley], *stenoloba* Shelley.

Additional Records. — *l. latior* — VA, Patrick Co., Blue Ridge Parkway at mile 174.3, M, 23 June 1984, R.L., and C. Hoffman (RLH); *l. munda* — SC, Spartanburg Co., Spartanburg, M, 3 October 1943, R.L. Wenzel (FMNH).

The *Quadrata* Group

The acropodites in this group are characterized by reduced medial flanges and simple tips that project inward into the arches at distinct angles from the distal zones. A lateral flange may or may not be present, but other acropodal specializations are absent. The prefemoral process is moderately long. The two species occupy small areas in the eastern Piedmont and Fall Zone of southern South Carolina.

Components. — *quadrata* Shelley, *laticurvosa* Shelley.

Additional Record. — *quadrata* — SC, Lexington Co., Leesville, M, 7 October 1949, L. Brodie (FMNH).

SIGMORIA (CROATANIA) Shelley, new status

Croatania Shelley, 1977:305-306. Hoffman, 1979:159.

Type species. — *Croatania catawba* Shelley, 1977, by original designation.

Diagnosis. — Paranota yellow or red, metaterga either uniformly black or with concolorous stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture, inserting between 7th legs; prefemoral process very large, usually extending beyond level of tip of distal zone; acropodites moderately thick and heavy to massive, well sclerotized, oriented normally on coxa with inner surface directed anteriomediad; basal zone with proximomedial edge expanded and irregularly notched, basalmost projection largest, spiniform; medial flange variable but laminate, located entirely on peak, expanded distad into lobe, latter sometimes detached from flange; lateral flange present, lobe-like, usually clearly demarcated from acropodite stem; tip blunt.

Remarks. — The subgenus *Croatania* occurs to the east and north of *Cleptoria* in piedmont South Carolina and ranges into south-central North Carolina. The center of diversity is the Broad River Valley of north-central South Carolina where *catawba, saluda,* and *simplex* are parapatric. The fourth species, *yemassee,* is allopatric in the outer Coastal Plain. The gonopods, widely separated and parallel *in situ* (see Fig. 46 of *simplex),* exhibit a number of specializations, the most obvious being an irregularly notched, proximomedial expansion of the basal zone, which varies in length and degree of jaggedness and is small and comparatively inconspicuous in *yemassee.* Three species — *catawba, saluda,* and *yemassee* — also have enormous prefemoral processes extending to or beyond the levels of the distal zones. Females of this group can be distinguished by the large, convoluted cyphopodal membrane, which protrudes through the medial corner of the aperture.

Croatania is composed of four species which are united in a single species group, the *catawba* group. They were illustrated and described in detail by Shelley (1977), and the gonopods are here redescribed in "sigmoid" terminology. New diagnoses and color descriptions are also presented along with new locality records for each species except *yemassee*. A discussion of variation is given for *simplex*.

Components. — *catawba* (Shelley), *saluda* (Shelley), *simplex* (Shelley), *yemassee* (Shelley).

Sigmoria (Croatania) catawba (Shelley), new combination

Croatania catawba Shelley, 1977:306-312, Figs. 1-2, 7, 11-12, 16. Filka and Shelley, 1980:28, Fig. 54.

The three new records of *catawba* add Cherokee County, South Carolina, to its known range and conform to the previous account of variation.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on peak and with yellow paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process massive, globose basally, bent ventrad distal to midlength and narrowing to acuminate tip, extending beyond level of tip of acropodite; latter thick and heavy, arch high and rounded, extending to but not beyond level of prefemoral process; basal zone with ridge on inner surface, proximomedial edge expanded into deeply notched plate, basalmost projection in form of short spine; anterior bend poorly defined; peak moderately long, gently curved; apical curve well defined; distal zone short, angling into arch, tip blunt; medial flange arising at anterior bend, expanding distad into triangular lobe on distal extremity of peak; lateral flange in form of thick lobe on proximal part of distal zone, well demarcated from acropodite stem.

Color in Life. — Paranota bright lemon yellow, occasionally orange; metaterga black, without stripes; collum with or without broad concolorous stripe along anterior margin.

Holotype Gonopods. — Prefemur moderate with massive process arising on dorsal side, subglobose basally, widest proximal to midlength and blackened along inner edge, bent ventrad at 2/3 length and tapering to acuminate tip; latter directed toward anterior bend, extending well beyond level of distal zone. Acropodite thick and heavy, well sclerotized, arch upright, a smooth, continuous curve overhanging but not extending beyond level of prefemoral process; basal zone with ridge on inner surface, proximomedial edge expanded into deeply notched plate, basalmost projection enlarged into short spine; anterior bend broad, poorly defined; peak moderately long, gently curved, apex at midlength; apical curve sharp, well defined; distal zone short, coplanar with basal zone, angling into arch and directed toward latter; tip blunt. Medial flange arising proximad on peak, expanded distad into triangular lobe on distal extremity. Lateral flange in form of thick, heavily sclerotized lobe on proximal part of distal zone, well demarcated from latter. Prostatic groove running along lateral side of ridge on

basal zone, crossing to lateral side of acropodite at anterior bend and continuing to terminal opening.

Distribution. — South-central piedmont North Carolina to north-central piedmont South Carolina (Shelley 1977). Specimens were examined from the following new localities:

SOUTH CAROLINA. — *Cherokee Co.,* 4.6 mi SE Blacksburg, along SC hwy. 5, 0.3 mi S jct. SC hwy. 68, F, 10 May 1977 (NCSM A1481). *Chester Co.,* 11.6 mi W Chester, Leeds Campground, Sumter Nat. For., 2M, F, 30 April 1977 (NCSM A1486); and 12.4 mi W Lowrys, along SC hwy. 9 at Broad R., 2M, 1 May 1977 (NCSM A1500). *Union Co.,* 0.1 mi N Jonesville, along SC hwy. 18, 2M, 2F, 2 May 1977 (NCSM A1505); 2.3 mi W Carlisle, along SC hwy. 24 at Cane Cr., 2M, 3F, 2 May 1977 (NCSM A1513); and 5.0 mi N Carlisle, along SC hwy. 86 at Neals Cr., Sumter Nat. For., 6M, 2F, 2 May 1977 (NCSM A1514).

Remarks. — The two males in sample A1500 from Chester County were found dead and lying on top of leaves. They had been recently decapitated by an unknown carnivore and were still pliable. One male lacked the head and collum, and the other had lost the head, collum, and segments 2 and 3. The bites were irregular and parts of the next segments had been destroyed, but there was no evidence of continuous chewing. The segments seem to have been removed by a single, clean bite, which stopped short of segment 5 and the anteriormost defensive glands. This situation is identical to that I reported for *Dicellarius t. talapoosa* (Chamberlin) from Cheaha Mountain, Alabama (Shelley 1984c).

Sigmoria (Croatania) saluda (Shelley), new combination

Croatania saluda Shelley, 1977:312-316, Figs. 3, 8, 13.

As with *catawba,* the new material of *saluda* conforms to previously known variation, but the range is expanded to encompass parts of Laurens, Lexington, Saluda, and Aiken counties, South Carolina. Its north-south distribution from the Enoree to the Savannah Rivers, is unchanged, but the area is extended eastward into the Fall Zone.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process large, sides parallel, curving broadly ventrad, apically bifurcate with medial component longer than lateral and extending beyond level of distal zone; acropodite thick and heavy, leaning dorsad and extending beyond level of prefemoral process; basal zone with proximomedial edge expanded into shallowly notched plate, basalmost projection enlarged into spine; anterior bend poorly defined; peak moderately long, gently curved; apical curve well defined; distal zone

short, angling into arch, tip blunt; medial flange arising at anterior bend, expanding distad into triangular lobe on distal extremity of peak and proximal part of distal zone; lateral flange in form of thick lobe on proximal part of distal zone, well demarcated from latter.

Color in Life. — Paranota usually entirely red, color occasionally restricted to peritremata; metaterga black, without stripes; collum with red strip along anterior margin.

Holotype Gonopods. — Prefemoral process not globose basally, of nearly equal width throughout, broadly curved ventrad, bifurcate apically, medial component longer than lateral component and extending beyond level of distal zone, directed toward anterior bend. Acropodite thick and heavy, well sclerotized, arch broad, a smooth continuous curve leaning dorsad and extending well beyond level of prefemoral process; basal zone without ridge, proximomedial edge expanded into shallowly notched plate, longer and more irregularly notched than in *catawba,* basalmost projection enlarged into short spine. Anterior bend broad, poorly defined; peak moderately long, gently curved, apex at midlength; apical curve sharp, well defined; distal zone short, coplanar with basal zone, angling into arch and directed toward prefemur; tip blunt. Medial flange arising at anterior bend, expanding distad into broadly rounded lobe on distal extremity of peak and proximal part of distal zone. Lateral flange in form of thick, heavily sclerotized lobe on proximal part of distal zone, well demarcated from latter. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Distribution. — Central and south-central piedmont South Carolina between the Enoree and Savannah Rivers, ranging east into the Fall Zone. Specimens were examined from the following new localities:

SOUTH CAROLINA. — *Laurens Co.,* 11.2 mi NE Clinton, along SC hwy. 72 at Duncan Cr., M, F, 9 May 1977 (NCSM A1564); 8.6 mi. S Clinton, along SC hwy. 38 at Little R., 3M, 9 May 1977 (NCSM A1565); and 2.0 mi. NE Cross Hill, along SC hwy. 560 at Campbell Cr., M, 9 May 1977 (NCSM A1566). *Greenwood Co.,* 8.4 mi. SW Ninety Six, along SC hwy. 702, 0.2 mi. W Saluda Co. line, M, 4 May 1977 (NCSM A1524). *Newberry Co.,* 16.0 mi. NE Newberry, along SC hwy. 45 at Enoree R., M, F, 3 May 1977 (NCSM A1517); and 6.3 mi. E Newberry, along US hwy. 176 at Mud Cr., 4M, 2F, 3 May 1977 (NCSM A1521); 11.5 mi. E Newberry, along US hwy. 176, 0.1 mi. S Pomaria, 3M, 2F, 14 July 1979 (NCSM A2804); 6.5 mi. SE Newberry, along SC hwy. 244, 0.5 mi. E jct. SC hwy. 315, M, F, July 1979 (NCSM A2806); and 9.0 mi. SE Newberry, along SC hwy. 403 at Camping Cr., M, F, 14 July 1979 (NCSM A2805). *Richland Co.,* 20.0 mi. NW Columbia, along US hwy. 176 at Wateree Cr., F, 14 July 1979 (NCSM A2803); and 14.0 mi. NW Columbia, along SC hwy. 244 at Hollingshead Cr., 3M, F, 14 July 1979 (NCSM A2802). *Lexington Co.,* West Columbia, M, 3F, 24 June 1958, collector unknown (FSCA); 13.0 mi. W Lexington, along SC hwy. 59 at Little Cr., 3M, 15 July 1979 (NCSM A2813); and 5.2 mi. NE Leesville, along SC hwy. 158, 0.3 mi. S jct. SC hwy. 54, 3M, 23 November 1977 (NCSM A1809). *Saluda Co.,* 4.0 mi. WNW Batesburg, along US hwy. 178 at Clouds Cr., 2M, 23 November 1977 (NCSM A1807); 6.0 mi. S Saluda, along SC hwy. 193, 0.1 mi. W jct. SC hwy. 119, 5M, 3F, 15 July 1979 (NCSM A2811); and 6.5 mi. E Saluda, along US hwy. 178, 0.2 mi. W jct. SC hwy. 29, M, F, 15 July 1979 (NCSM A2811). *Edgefield Co.,* 1.9 mi. ENE Trenton, along SC hwy. 75 at Tiger Cr., 3M, 2F, 23 November 1977 (NCSM A1804); and 7.5 mi. S Edgefield, along SC hwy. 34 at Double Branch Cr., M, 16 July 1979 (NCSM A2821). *Aiken Co.,* Lexington Co. line on SC hwy. 109 at Chinquapin Cr., 2M, F, 15

July 1979 (NCSM A2818); and North Augusta, along SC hwy. 230, 1.7 mi. E I-20, 2M, 2F, 17 September 1980 (NCSM A3509).

Sigmoria (Croatania) simplex (Shelley), new combination   Figs. 46-48

Croatania simplex Shelley, 1977:316-319, Figs. 4-5, 9, 14.

Priority for the name *simplex* is with this species, proposed four years before the one herein renamed *inornata (Sigiria)*. The original description of *simplex* was based only on the type series from Chester County, South Carolina, and the range could not be reported, nor could variation be discussed aside from that demonstrated by paratypes.

Diagnosis. — A moderate-size species of *Sigmoria* with short medial flange located on distal extremity of peak or proximal part of distal zone and with yellow or red paranota, metaterga with or without narrow, concolorous transverse stripes; gonopods with following diagnostic characters: prefemoral process moderately long, curving broadly ventrad, apically acuminate or bifurcate; acropodite moderately thick, arch flattened or a smooth, continuous curve, overhanging and extending beyond level of prefemoral process; basal zone with proximomedial edge expanded into variably notched plate, basalmost projection largest; anterior bend poorly defined; peak moderately long, gently curved or flattened; apical curve variably defined; distal zone moderately long, curving broadly into arch or extending ventrad from peak and bent abruptly into arch at midlength, apically acuminate; medial flange represented by distal lobe and short preceding lamella, either located on distal extremity of peak or arising there and terminating near midlength of distal zone; lateral flange either absent or represented by widening in proximal portion of distal zone.

Color in Life. — Paranota bright lemon yellow, occasionally red; metaterga black, with or without concolorous stripes along caudal edges; collum with stripe along anterior margin.

Holotype Gonopods. — Prefemoral process moderately long (Fig. 47), terminating well below level of distal zone, crescent shaped, widest at 1/3 length, then tapering smoothly and continuously to acuminate tip, latter directed toward anterior bend. Acropodite moderately thick and heavy, arch upright, a smooth, continuous curve overhanging and extending beyond level of prefemoral process; basal zone without ridge, basal proximomedial expansion short, shallowly notched, basalmost projection enlarged into short spine; anterior bend broad, poorly defined; peak relatively short and high, gently rounded, apex at midlength; apical curve broad, poorly defined; distal zone moderately long, curving broadly into arch, tapering smoothly and continuously to acuminate tip; latter directed toward anterior bend. Medial flange short, inconspicuous, represented only by short, blunt tubercle and short attached lamella at level of apical curve, this homologous to lobe of *catawba*. Lateral flange indistinct, represented by broad rounded area at midlength of distal zone. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.
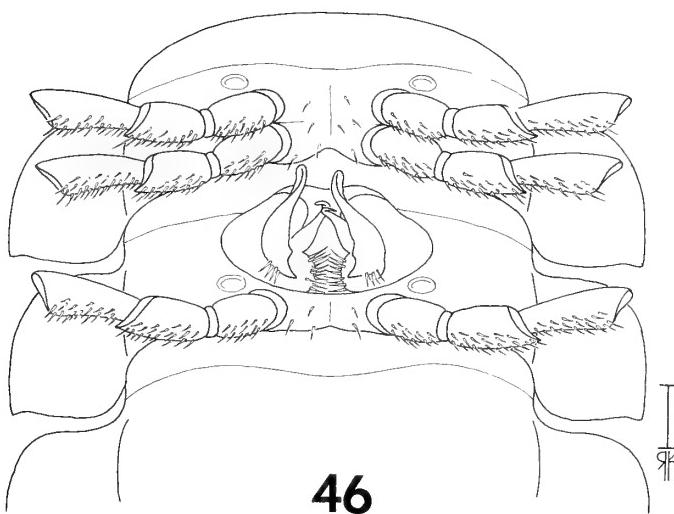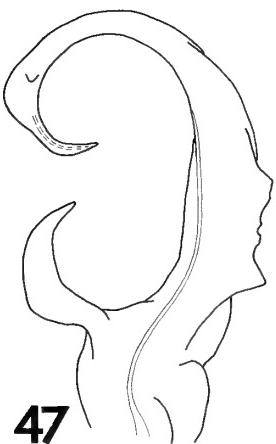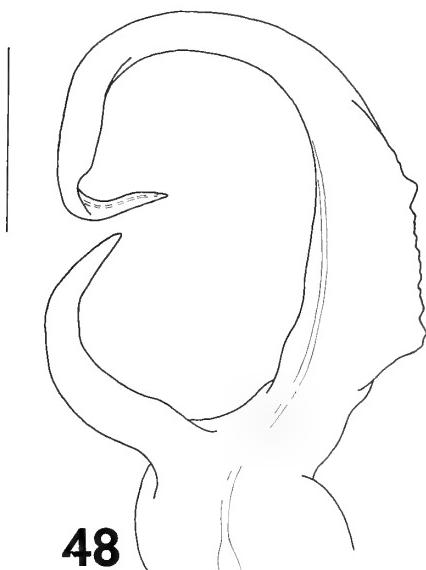
FIGS. 46-48. *Sigmoria (Croatania) simplex.* 46, gonopods *in situ,* ventral view of male from Fairfield Co., SC. 47, telopodite of left gonopod of holotype, medial view. 48, telopodite of left gonopod of male from Richland Co., SC. Scale line for fig. 76 = 1.00 mm; line for other figs. = 1.00 mm for 77; 0.64 mm for 48.

Variation. — Some specimens have yellow stripes along the caudal margins of the metaterga, whereas others, like the types, lack these markings. Both patterns were found 4.2 mi. N Columbia (samples A2800-2801), but there were no detectable anatomical differences. Material from Berkeley and Orangeburg counties had red paranota and stripes.

The gonopods of eastern populations vary considerably from the types, and a representative example is shown in Figure 48. Aside from occasional bifurcate individuals, as found in the type series, the prefemoral process is generally of the same shape throughout the range, although it becomes longer and narrower in eastern populations. In the Kershaw County males it projects beyond the level of the distal zone. The proximomedial expansion is shorter and less jagged in some males, and this does not conform to any geographic pattern. The medial flange, however, is broad and laminate in eastern forms, and the distal zone likewise projects inward into the arch of the acropodite at a sharper angle, often at right angles. The configuration shown in Figure 12 is actually more common and representative of *simplex* than that of the holotype, which is restricted to the northwestern range periphery and may represent a terminal population effect. Thus, the situation is similar to that in *macra (Cleptoria),* where the holotype is atypical for the species.

Distribution. — Farifield, Richland, Kershaw, Orangeburg, and Berkeley counties can be added to the distribution of *simplex,* which is now known from both the Piedmont and Coastal Plain of South Carolina. The type locality is the northernmost, as I have not found the species in Union, York or Lancaster counties. The range abuts that of *catawba* in Chester County, and in Richland County, *simplex* is segregated from *saluda* by the Broad River. Here and in Fairfield County the waterway is the western limit, but northern populations in Chester County do not extend to the river, being replaced on the eastern side by *catawba.* Material was examined from the following localities:

SOUTH CAROLINA. — *Chester Co.,* 7.2 mi. SE Chester, along SC hwy. 44, 0.7 mi. W jct. SC hwy. 347, F, 1 May 1977 (NCSM A1492); and 7.2 mi. SW Chester, along SC hwy. 42 at Sandy R., 4M, F, 1 May 1977 (NCSM A1502). *Farifield Co.,* 16.8 mi. NW Winnsboro, along SC hwy. 215, 0.5 mi. N jct. SC hwy. 302, 2M, 2F, 3 May 1977 (NCSM A1516); 12.0 mi NW Winnsboro, along SC hwy. 28 at Mobley Cr., 2M, 13 July 1979 (NCSM A2793); 7.0 mi. NW Winnsboro, along SC hwy. 303, 1.5 mi. N jct. SC hwy. 22, 2M, 2F, 13 July 1979 (NCSM A2792); 13.0 mi. SW Winnsboro, along SC hwy. 46 at Sawney's Cr., M, 2F, 13 July 1979 (NCSM A2788); 10.5 mi. SW Winnsboro, along SC hwy. 213 at Little R., 3M, 2F, 13 July 1979 (NCSM A2794); 9.5 mi. S Winnsboro, along SC hwy. 64 at Little Cedar Cr., 5M, F, 13 July 1979 (NCSM A2796); and 9.0 mi. NE Winnsboro, along SC hwy. 234 at Wateree Cr., M, 13 July 1979 (NCSM A2791). *Kershaw Co.,* 11.0 mi. NNW Camden, along SC hwy. 40 at Flat Rock Cr., 2M, F, 12 July 1979 (NCSM A2789). *Richland Co.,* 15.0 mi. NNE Columbia, along

SC hwy. 54 at Five Mile Cr., M, F, 13 July 1979 (NCSM A2798); 15.0 mi. NNW Columbia, along SC hwy. 967 at Horse Cr., 3M, F, 13 July 1979 (NCSM A2797); 12.0 mi. NNW Columbia, along SC hwy. 59, 0.1 mi. N jct. SC hwy. 215, M, 23 November 1977 (NCSM A1811); 7.0 mi. N Columbia, along SC hwy. 61 at North Branch Cr., 9M, 7F, 14 July 1979 (NCSM A2800-A2801); and 3.0 mi. N Columbia, along US hwy. 321 at Crane Cr., 2M, F, 14 July 1979 (NCSM A2799). *Orangeburg Co.,* Santee State Park, M, 9 September 1980 (NCSM A3494). *Berkeley Co.,* 20.0 mi. W Moncks Corner, along SC hwy. 27, 10.0 mi. N jct. I-26, bluff area of Four Holes Swamp Sanctuary, 4M, 2F, 9 September 1980 (NCSM A3493).

Remarks. — The *in situ* gonopodal configuration in this and other species of *Croatania* is the parallel arrangement shown in Figure 46.

Sigmoria (Croatania) yemassee (Shelley), new combination

Croatania yemassee Shelley, 1977:319-321, Figs. 6, 10, 15.

Sigmoria yemassee is still known only from the two collections cited in 1977. I have extensively surveyed the environments in southeastern South Carolina and visited the type locality twice and the other site once at the
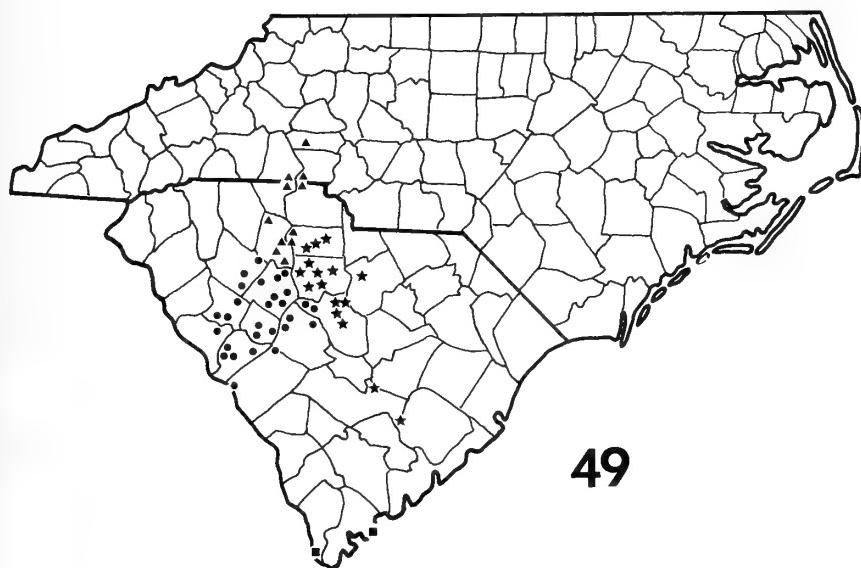
Fig. 49.   Distribution of the subgenus *Croatania* in North and South Carolina. Triangles, *catawba;* stars, *simplex;* dots, *saluda;* squares, *yemassee.*

proper times of the year, without finding a single individual. The color in life is therefore unknown.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on distal extremity of basal zone and proximal part of distal zone; gonopods with following diagnostic characters: prefemoral process large, bisinuately curved, bent ventrad apically and narrowing to acuminate tip, extending to level of distal zone; acropodite thick and heavy, arch high and narrowly rounded, extending just beyond level of prefemoral process; basal zone slightly expanded, with small denticulations on proximomedial edge, not noticeably expanded; anterior bend poorly defined, peak rounded, short and high, apical curve well defined; distal zone very short, angling into arch, apically blunt; medial flange in two parts, a narrow, inconspicuous lamina on distal extremity of basal zone and narrow, rhomboidal projection on distal extremity of peak, representing distal lobe of flange in *catawba;* lateral flange a short quadrate lobe on distal zone, margin finely serrate.

Color in Life. — Unknown.

Holotype Gonopods. — Prefemoral process upright, bisinuately curved, not globose basally, bent ventrad apically and narrowing abruptly to acuminate tip; latter directed toward midpoint of telopodite. Acropodite moderately thick and heavy, well sclerotized; arch high and narrowly rounded, upright, slightly overhanging prefemoral process; basal zone without ridge, proximomedial expansion short, with only small denticulations, none enlarged; anterior bend poorly defined; peak short, apex at midlength; apical curve sharp, well defined; distal zone short, projecting inward for short distance into arch, tip broadly rounded and directed toward basal zone. Medial flange located on distal extremity of basal zone and proximal part of distal zone; former a short, narrow, inconspicuous lamina; latter a linear rhomboidal projection. Lateral flange represented by quadrate lobe, margin finely serrate. Prostatic groove crossing from medial to lateral sides at midlength of basal zone, continuing to subterminal opening.

SIGMORIA (CLEPTORIA) Chamberlin, new status

Cleptoria Chamberlin, 1939:9. Chamberlin and Hoffman, 1958:28. Hoffman, 1967:5-7; 1979:158. Jeekel, 1971:254.
Brevigonus Shelley, 1980a:32-34; 1981b:54-55. **NEW SYNONYMY.**

Type species. — Of *Cleptoria, C. macra* Chamberlin, 1939, by original designation; of *Brevigonus, Cleptoria shelfordi* Loomis, 1944, by original designation.

Diagnosis. — Paranota red, metaterga either uniformly black or with conclorous red stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture, inserting between 7th legs; prefemoral process moderate to small, frequently ab-

sent; acropodites moderately thick to massive, heavily sclerotized, oriented normally on coxa; basal zone with or without variable basal spine on outer surface; medial flange variable in shape and location, moderately laminate to a thickened swelling of medial surface of acropodite stem, located on basal zone and / or peak, occasionally with suggestion of distal lobe; lateral flange occasionally laminate but usually swollen, thickened, and lobe-like, poorly demarcated from acropodite stem, located more ventrad than laterad, forming highest point of acropodite arch; tip variable.

Remarks. — *Cleptoria* occurs chiefly in piedmont South Carolina and Georgia, and its species have the largest bodies and the most massive, heavily sclerotized acropodites in the genus. The medial flanges are usually thick, stiff projections instead of thin, flexible lamellae as in other subgenera. Likewise, only one species has a laminate lateral flange; otherwise the structure is a swollen, broadly rounded, and poorly demarcated lobe on the proximal part of the distal zone. It typically projects ventrad more than laterad and forms the highest point of the acropodal arch. The distal zone is long and blade-like in one species and is absent from another. In forms with lobe-like lateral flanges, the region is short, broad, and directed perpendicularly from the peak, imparting an overall "bird's head" appearance to the acropodite (Bollman 1888).

Cleptoria presents the most difficult taxonomic decisions in *Sigmoria s. lat.,* particularly with the highly variable South Carolina forms. Central and southern populations of *macra* possess sharply acute spurs on the outer surfaces of the peaks as do adjacent populations of *shelfordi,* the parapatric southern form with a shortened acropodite (lacking the distal zone and apical curve). This condition could derive from that in *macra* by reduction of the lateral flange (lobe) and the short distal zone, but the picture is complicated by the random absence of the spur in *shelfordi.* Additionally, random males of *shelfordi* have spines on the basal zones, which are absent from *macra.* Thus, two principal variants of *shelfordi* exist (Shelley 1980a). Its range is unequally divided by *arcuata,* which has a long distal zone and basal acropodal spine. *Sigmoria (Cleptoria) robusta,* with a swollen, rounded lateral flange and a short distal zone, occurs west of *arcuata.* Its acropodite is heavier than that of *macra* and is similar to the Georgia species; it also lacks the spur but has the basal spine. Thus in South Carolina, forms with shortened acropodites (the variants of *shelfordi*) connect forms with "bird's head" acropodites (*robusta* and *macra*), which in turn are segregated elsewhere by a form with a long curved distal zone (*arcuata*) that also bisects the range of the first form (*shelfordi*)! Features like the basal spine and midlength spur traverse the sharp boundaries between the overall acropodal forms. The spine occurs in *robusta, arcuata,* and ran-

domly in *shelfordi;* the spur also occurs randomly in *shelfordi* and in all populations of *macra* except the northern ones.

The picture is clearer in Georgia because there is only one acropodal form, the "bird's head." Hoffman (1967) recognized three species, and I concur although the status of *bipraesidens,* known only from the holotype, could change when more material is available from northwest of Athens. Unlike the parapatric *rileyi, bipraesidens* lacks the spine on the basal zone; has a longer, more acute, and more strongly indented distal zone; and the entire medial surface of the peak is thickened to represent the flange. *Sigmoria (Cleptoria) abbotti,* the parapatric species to the east of *rileyi,* is most common along the Savannah River between Hart and Burke counties. It differs from *rileyi* in having a prefemoral process; an expanded, laminate anterior margin of the basal zone; a thin, narrow, indistinct medial flange; and a stronger basal spine. Similarities in the basal zones and prefemora of *abbotti* and *robusta* suggest prior connection and that the ancestral range curved northward from Hart County. Following segregation by the Savannah River, the forms diverged as revealed by the outer margins of the distal zones, rounded and continuous in *robusta* and strongly indented in *abbotti.* Thus, the "bird's head" acropodal configuration and the spine on the basal zone traverse the Savannah River, whereas the spur, the short acropodite of *shelfordi,* and the long curved one of *arcuata* are restricted to the northern side. The last three conditions evolved subsequent to the "bird's head" configuration, which antedates the present course of the Savannah River. Equally interesting are small, allopatric populations of *rileyi* in eastern and central Alabama. Reasonably thorough searches have failed to produce *rileyi* in western Georgia, and the main range is disjunct from that in eastern Alabama by about 100 miles. Thus, geographical isolation brought about by the Savannah River seems to have promoted divergence of *robusta* and *abbotti,* which are only about 20 miles apart, but isolation has not affected the Alabama populations of *rileyi,* which are also segregated by major waterways and five times as much distance!

A complete description is presented for *robusta,* but only diagnoses and color statements are provided for *shelfordi* and *arcuata,* since their gonopods were characterized in "sigmoid" terminology by Shelley (1980a, 1981b). Hoffman (1967) published full descriptions for *rileyi, abbotti, bipraesidens,* and *macra,* so only diagnoses, color statements, and redescriptions of the gonopods are needed. The species of *Cleptoria* form a homogeneous unit, and thus there is only one, the *rileyi,* species group.

Components. — *rileyi* (Bollman), *macra* (Chamberlin), *shelfordi* (Loomis), *bipraesidens* (Hoffman), *abbotti* (Hoffman), *arcuata* (Shelley), *robusta* new species.

Sigmoria (Cleptoria) rileyi (Bollman), new combination   Figs. 50-52

Fontaria rileyi Bollman, 1888:345. Attems, 1938:167.
Cleptoria rileyi: Chamberlin, 1939:10. Chamberlin and Hoffman, 1958:28.
Cleptoria rileyi rileyi: Hoffman, 1967:12-15, Figs. 2, 7-8.
Cleptoria rileyi alabama Hoffman, 1967:16-17, Figs. 9-10. **NEW SYNONYMY.**

Hoffman (1967) provided a detailed description and illustrations of the holotype of *rileyi* along with a short account of the allopatric population in Lee County, Alabama. Toward the end of the present study a nearly identical male was obtained from Jefferson County, about 100 miles northwest of Lee County. I find no meaningful differences between the Alabama forms and those in central Georgia and no justification for taxonomic recognition. The following supplemental account characterizes the sternal process of the holotype and its gonopods in "sigmoid" terminology, and addresses aspects of variation, ecology, and distribution. I also present additional drawings of the gonopods including one from ventral view, which shows the flange protruding on the medial side.

Type specimens. — Male holotype (NMNH) collected by L.M. Underwood, August 1887, at Macon, Bibb Co., GA.

Diagnosis. — A large species of *Sigmoria* with medial flange on peak and with red paranota, metaterga without stripes; gonopods with following diagnostic characters: prefemoral process absent; acropodite massive, arch flattened and squared, extending well beyond level of prefemur; basal zone moderately long and broad, with small basal spine on caudal edge; anterior bend well defined; peak long, flat, constricted distad; apical curve well defined; distal zone short, directed perpendicularly from peak, outer margin moderately indented, sides narrowing apically to subacuminate tip; medial flange thick but relatively laminate, arising on proximal portion of peak, expanding into broadly rounded distal lobe near midlength of peak; lateral flange represented by thick, broadly rounded lobe on proximal part of distal zone, protruding ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life. — Paranota red; metaterga dark glossy black, without stripes along caudal edges; collum also without stripes along either margin.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae (Hoffman, 1967, Fig. 2).

Gonopods *in situ* with acropodites projecting anteriad from aperture, extending forward in parallel arrangement over anterior margin to between 7th legs. Gonopod structure as follows (Figs. 50-52): Prefemoral process absent. Acropodite massive, heavily sclerotized, forming rectangular arch overhanging and extending well beyond prefemur; basal zone moderately broad, anterior edge slightly thinner than caudal but not especially laminate or expanded, outer margin wider basally with short spiniform projection; anterior bend sharp, well defined, approximately a right angle; peak relatively long, straight, and level, constricted on both margins

at distal extremity; apical curve sharp, well defined; distal zone short, with distolateral striae, outer margins moderately indented, margins gently curved and narrowing to blunt tip; latter directed toward coxa. Medial flange relatively thick, moderately laminate, arising proximally
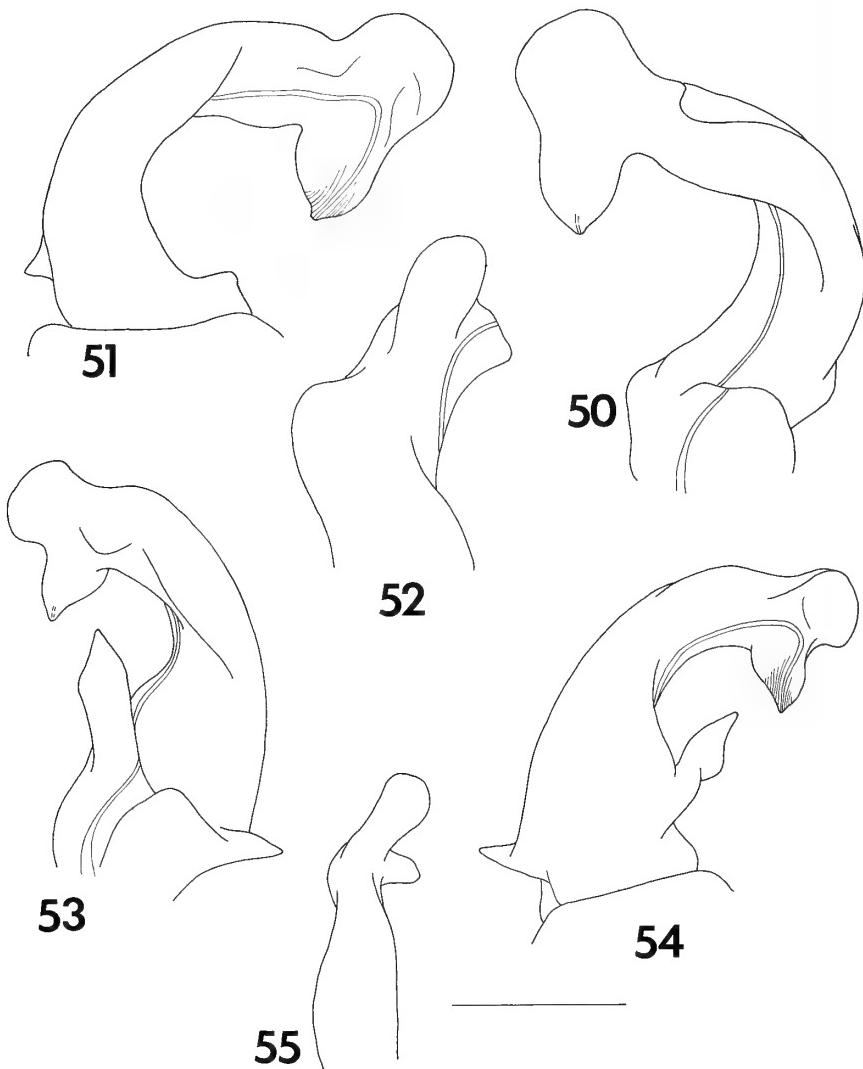
FIGS. 50-55. 50-52, *Sigmoria (Cleptoria) rileyi*. 50, telopodite of left gonopod of holotype, medial view. 51, the same, lateral view. 52, the same, ventral view. 53-55, *Sigmoria (Cleptoria) abbotti*. 53, telopodite of left gonopod of male from Lincoln Co., GA, medial view. 54, the same, lateral view. 55, the same, ventral view. Scale line = 1.00 mm for all figures.

on peak, curving sharply mediad and forming broadly rounded lobe near midlength of peak, terminating abruptly distal to lobe. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad forming highest point of acropodite arch, poorly demarcated from acropodite stem by only slight impression in distal zone. Prostatic groove crossing to lateral side at anterior bend, curving onto distal zone and opening terminally.

Variation. — Gonopodal variation in *rileyi* is negligible. Males from central Georgia are nearly identical to each other, and the only difference in those from Alabama is a slight enlargement on the anterior surface of the prefemur in some individuals, which suggests a vestigial prefemoral process.

Ecology. — *Sigmoria (Cleptoria) rileyi* occurs under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — Comprised of three allopatric populations, one in central Georgia, and one in Lee and one in Jefferson counties, Alabama (Fig. 68). These areas are in the Piedmont Plateau, the Fall Zone, and the Cumberland Plateau, respectively. The Georgia population occupies a linear area roughly 60 miles long between I-85 and I-75, and three trips to sections of Georgia west of that shown in figure 68 produced specimens of *Dynoria medialis* Chamberlin and *Sigmoria (Cheiropus) persica,* but none of *rileyi.* At best the species is uncommon here. Material was examined from the following new localities:

GEORGIA. — *Clarke Co.,* Athens, 3M collected in June, July, and October 1948-1972 (FSCA). *Oconee Co.,* Bogart, 2M, 14 October 1973, R.L. Duffield (RLH). *Morgan Co.,* Hard Labor Creek St. Pk., 4M, 3F, 15 June 1958, N.B. Causey (FSCA). *Putnam Co.,* 7 mi. S Eatonton, Sinclair Lake Rec. Area, Oconee Nat. For., M, 20 November 1977 (NCSM A1786); and 7 mi SE Monticello, along GA hwy. 212 at Jasper co. line, 3M, 20 November 1977 (NCSM A1788).

ALABAMA. — *Lee Co.,* Chewacla St. Pk., 7M, 4F, 21 May 1980 (NCSM A3122); Auburn, 8M, 13 June 1959, N.B. Causey (FSCA) and Auburn Univ. campus, 2M, June-July 1973, F.M. Scale and R. Russell (AU). *Jefferson Co.,* 10 mi. S Birmingham, along AL hwy. 150, 1.2 mi. W jct. US hwy. 31, M, Fall 1984, R.E. Ashton (NCSM A4228).

Sigmoria (Cleptoria) abbotti (Hoffman), new combination   Figs. 53-55

Cleptoria abbotti Hoffman, 1967:18-21, Figs. 13-16.

This species was known from only two localities when it was described and illustrated by Hoffman (1967). Much more material is available now, providing insight into variation and distribution. The lateral flange, which Hoffman called the subapical lobe, seems overemphasized in his drawings, and I therefore present figures of a male from Lincoln County, Georgia, approximately 55 miles NW of the type locality.

Type specimens. — Male holotype (NMNH) and one male and one female paratype collected by L. Hubricht, 22 May 1960, from 5 mi. SW Waynesboro, Burke Co., GA. Male and female paratypes deposited in RLH.

Diagnosis. — A large species of *Sigmoria* with medial flange extending from distal extremity of basal zone to midlength of peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: projection of prefemur present, either distinct process or fold of anterior lamina of basal zone; acropodite massive, leaning over and extending beyond level of prefemoral process; basal zone very broad, inner surface convex with thin, laminate lateral margin and with short, acute, basal spine on caudal margin; anterior bend poorly defined; peak short; apical curve well defined; distal zone short, directed perpendicularly from peak, outer margin strongly indented, sides tapering to subacuminate tip; medial flange thick, narrow, and inconspicuous, not particularly laminate, terminating in slight lobe on distal part of peak; lateral flange represented by thick, broadly rounded lobe on proximal portion of distal zone, protruding ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life. — Paranota red; metaterga dark glossy black, without stripes along caudal edges; collum also without stripes.

Holotype. — 4th sternal process long, apically divided, longer than widths of adjacent coxae (Hoffman 1967, Fig. 4).

Gonopods *in situ* with acropodites projecting anteriomediad from aperture, overlapping in midline and extending forward over anterior margin to between 7th legs. Gonopod structure as follows (Figs. 53-55): Prefemur with rounded lobe on medial surface; prefemoral process short and conical, directed toward apical curve. Acropodite massive, heavily sclerotized, leaning over and extending well beyond level of prefemoral process; basal zone broad, with short, acute spine proximad on outer margin, medial surface convex with anterior edge expanded into thin lamina; anterior bend broad, poorly defined; peak short and thick; apical curve sharp, well defined; distal zone short, with distolateral striae, outer margins gently curved and narrowing to subacuminate tip; latter directed toward coxa. Medial flange thick, narrow, and inconspicuous, arising on basal zone, terminating at midlength of peak, latter with slight thickening on medial surface distal to flange representing lobe of latter. Lateral flange lobelike, located on proximal part of distal zone, broadly rounded and produced ventrad, leaning laterad and demarcated from distal zone by slight depression. Prostatic groove crossing to lateral side at anterior bend, curving onto distal zone and terminating apically.

Variation. — The anterior edge of the basal zone is thin and laminate, and in many males, what is called the prefemoral process is really just the expanded, folded proximal end of this lamina, which appears as a separate projection because its profile is viewed in medial perspective. Few males in addition to the types have a truly separate subconical process (Hoffman 1967) that extends clearly beyond the margin of the lamina. The structure occurs randomly throughout the range, being found on males from Hart,

Elbert, Lincoln, and Burke counties. The medial flange, inconspicuous in all specimens, also varies randomly. There is a slight thickening of the medial surface of the peak at the level of the apical curve, which is not really visible in medial view and is best seen from the ventral perspective. As in *rileyi,* I think this represents the distal lobe of the medial flange, and it is continuous with the medial flange in males from Columbia County. The size of the spine on the outer surface of the basal zone also varies, but the projection on the 4th sternum is longer than the widths of the adjacent coxae in all individuals.

Ecology. — *Sigmoria (Cleptoria) abbotti* is typically found in predominantly hardwood areas under thin layers of leaves on relatively hard substrates near water sources. I also encountered it in similar spots in predominantly pine woods, under the few deciduous trees in the area.

Distribution. — The Piedmont Plateau and the inner edge of the Coastal Plain along the southern side of the Savannah River from Hart to Burke counties, Georgia. The area is about 85 miles long, but *abbotti* is most common between US highways I-85 and I-20. It extends to 30 miles south of the river, there abutting the range of *rileyi* (Fig. 68). Material was examined from the following new localities:

GEORGIA. — *Oconee Co.,* Watkinsville, M, F, 26 March 1959, W. Tarpley (FSCA). *Hart Co.,* 8 mi. ESE Hartwell, along co. rd. 1724 at Little Cedar Cr., 2M, 20 July 1979 (NCSM A2841). *Elbert Co.,* 11 mi. NNE Elberton, along GA hwy. 368 at Pickens Cr., 2M, F, 20 July 1979 (NCSM A2840); Nancy Hart St. Pk., M, F, 19 July 1979 (NCSM A2938). *Oglethorpe Co.,* Oconee Nat. For., 3M, 8 June 1973, R.L. Duffield (RLH). *Greene Co.,* 10.8 mi. NW Greensboro, Oconee R. Rec. Area, Oconee Nat For., 2M, F, 22 November 1977 (NCSM A1799). *Lincoln Co.,* 6 mi. N. Lincolnton, along GA hwy. 79 at Mills Cr., 4M, F, 19 July 1979 (NCSM A2835); 2.6 mi. NW Lincolnton, along GA hwy. 904 at Soap Cr., 2M, F, 19 July 1979 (NCSM A2832); and 6 mi. SE Lincolnton, along GA hwy. 220 at Cherokee Cr., M, 2F, 19 July 1979 (NCSM A2830). *Columbia Co.,* Mistletoe St. Pk., 2M, F, 18 July 1979 (NCSM A2825); 10 mi. NE Appling, along US hwy. 221 at Clark Hill Dam, 2M, F, 19 July 1979 (NCSM A2828); 15.5 mi. N. Harlem, along GA hwy. 104, 5M, 19 July 1979 (NCSM A2829); 10 mi. NW Augusta, along GA hwy. 28, 0.1 mi. E Savannah R., 2M, F, 13 September 1980 (NCSM A3513); and Augusta Canal St. Pk., 3M, 13 September 1980 (NSCM A3511).

Remarks. — The female from Lincoln County, assigned to *rileyi* by Hoffman (1967), is here referred to *abbotti,* the only species in this county.

Although similar, I think that *abbotti* and *rileyi* are reproductively isolated because parapatric populations in Oconee, Morgan, Greene, and Oglethorpe counties maintain their respective identities and show no evidence of hybridization. *Sigmoria (Cleptoria) abbotti* has a prominent basal spine on the outer surface of the basal zone, whereas that in *rileyi* is barely detectable. The anterior margin of this section, expanded and laminate in *abbotti* is enlarged in some males to represent the prefemoral

process. *Sigmoria (Cleptoria) rileyi,* however, lacks both the lamina and a prefemoral process; its medial flange is also more distinct and laminate than that of *abbotti.*

Sigmoria (Cleptoria) bipraesidens (Hoffman), new combination Figs. 56-59

Cleptoria bipraesidens Hoffman, 1967:16-17, Fig. 11

Hoffman (1967) provided a brief description of the holotype and only known specimen of this species, but he did not illustrate the process of the 4th sternum nor show a medial view of the gonopods. I therefore present these figures along with lateral and ventral views of the gonopods and selected anatomical details. No additional material is available to provide information on variation or distribution.

Type specimen. — Male holotype (NMNH) collected by L. Hubricht, 4 April 1953, at Jefferson, Jackson Co., GA.

Diagnosis. — A large species of *Sigmoria* with thickening on medial surface of peak representing medial flange and with red paranota and transverse metatergal stripes; gonopods with following diagnostic characters: prefemoral process absent; acropodite massive, arch flattened and extending well beyond level of prefemur; basal zone without trace of spine on outer surface; anterior bend broad, poorly defined; peak relatively long, flat; apical curve well defined; distal zone moderately long, outer margin strongly indented, directed perpendicularly from peak, inner edge linear, outer edge converging to acuminate tip; medial flange non-laminate, a thickening on peak, narrowest along inner surface and widest on outer; lateral flange represented by thick, broadly rounded lobe on proximal part of distal zone, protruding ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life (Hoffman 1967). — Paranota red; metaterga black with red transverse stripes along caudal edges; collum with red stripes along both anterior and posterior margins.

Holotype. — Width across genal apices 4.9 mm; genae with distinct central impressions. Facial setae with epicranial, interantennal, genal, and frontal series absent; clypeal about 12-12, labral about 16-16.

Terga smooth, polished, becoming moderately coriaceous on paranota. Latter moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 8, blunt on 9-14, becoming progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surfaces; ozopores located near midlength, opening dorsolaterad.

Sternum of segment 4 with large, apically divided process between 3rd legs, longer than widths of adjacent coxae (Fig. 56); that of segment 5 with two long, paramedial, basally coalesced knobs between 4th legs, length equal to widths of adjacent coxae, and low, flattened, elevated areas between 5th legs; that of segment 6 with shallow, convex, depression between 7th legs to accommodate curvatures of acropodites. Coxae with low, blunt tubercles arising on

postgonopodal legs of segment 9, becoming sharper and more acute posteriorly; prefemoral spines arising on segment 5, becoming longer and sharper caudally.

Gonopodal aperture ovoid, 4.4 mm wide and 2.7 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. *In situ* arrangement of gonopods
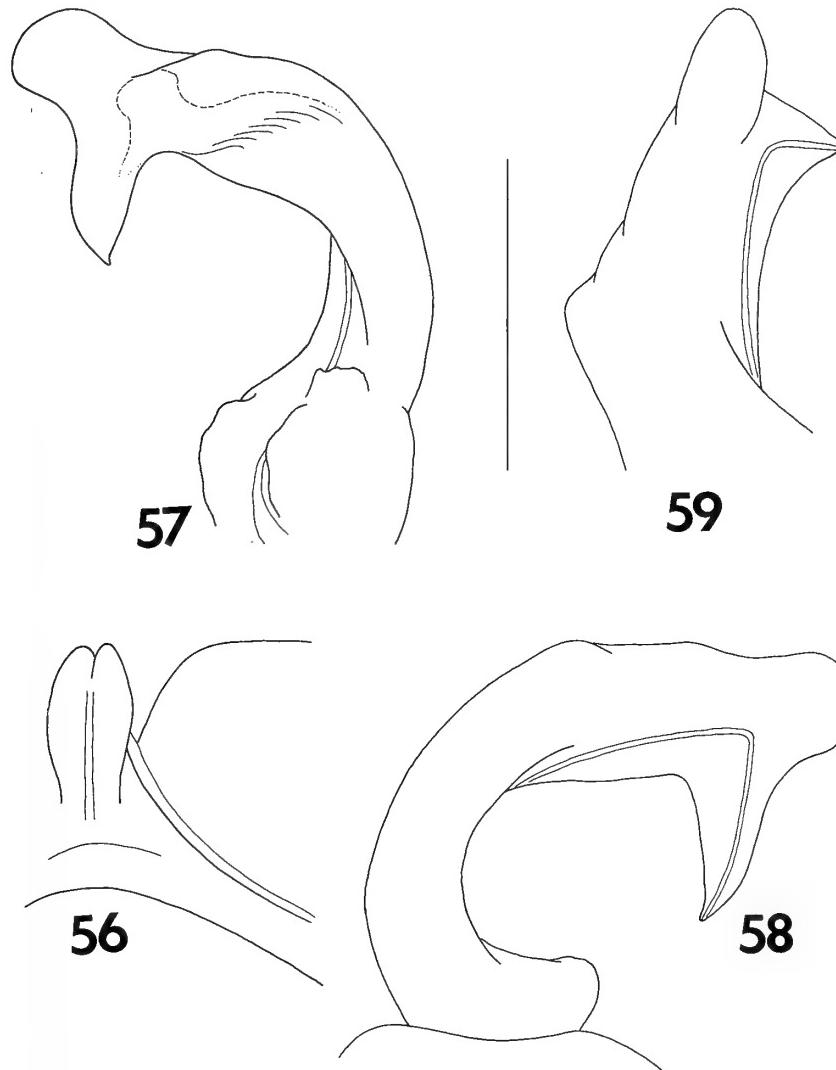
Figs. 56-59. *Sigmoria (Cleptoria) bipraesidens.* 56, process of 4th sternum of holotype, caudal view. 57, telopodite of left gonopod of the same, medial view. 58, the same, lateral view. 59, the same, ventral view. Scale line = 1.00 mm for 56 and 59; 1.60 mm for 57-58.

unknown. Gonopod structure as follows (Figs. 57-59): prefemoral process absent. Acropodite thick and massive, heavily sclerotized, forming rectangular arch, overhanging and extending well beyond prefemur; basal zone moderately broad, without spine on outer surface, with short blunt, basal lobe on medial side; anterior bend sharp, well defined, approximately a right angle; peak relatively long, straight, and level, constricted very slightly on both margins on distal extremity; apical curve sharp, well defined; distal zone moderately long, directed perpendicularly from peak, outer margin strongly indented, inner edge linear, outer straight proximally then curving beyond midlength and converging with inner at acuminate tip; latter directed toward coxa. Medial flange represented by thickened non-laminate area along entire width of peak, beginning proximally and terminating on distal extremity, narrowest on inner margin, widest on outer. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad forming highest point of acropodite arch, leaning slightly laterad and demarcated from distal zone by slight depression. Prostatic groove crossing to lateral side at anterior bend, bending sharply (90°) onto distal zone and opening terminally.

Remarks. — The striped color pattern of *bipraesidens* (Hoffman 1967) should be confirmed in fresh material, since this is the only reported individual in *Cleptoria* with metatergal markings.

The differences between *bipraesidens* and *rileyi* are even less distinct than those between the latter and *abbotti*. However, their close geographical proximity combined with the longer distal zone and non-laminate medial flange of *bipraesidens* suggest reproductive isolation. The status of *bipraesidens* should be reviewed when more material is available.

Sigmoria (Cleptoria) robusta Shelley, new species   Figs. 60-63

Type specimen. — Male holotype (NCSM A1553) and one male and one female paratypes collected by R.M. Shelley, 7 May 1977, in Oconee Co., SC, 10.8 mi. SW Seneca, along SC highway 168, 0.3 mi. S junction with SC highway 86. Male and female paratypes (NCSM A2061) collected by R.M. Shelley and W.B. Jones, 10 June 1978, in Oconee Co., 5.7 mi SE Oakway, along SC highway 66 at Beaverdam Cr. SC. Male paratype deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* with medial flange extending between distal extremity of basal zone and proximal portion of distal zone and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process short, blunt, and narrow; acropodite massive, arch flattened and extending beyond level of prefemoral process; basal zone very broad, inner surface convex and lateral margin thin and laminate, with sharply acute basal spine on caudal edge; anterior bend broad, poorly defined; peak flattened but rising to distal apex; apical curve sharp well defined; distal zone short, directed perpendicularly from peak, outer margin not indented, sides curving broadly to blunt tip; medial flange thick but relatively laminate, long, narrow, and in-

conspicuous, with broadly rounded distal lobe; lateral flange represented by thick broadly rounded lobe on proximal part of distal zone, produced ventrad, demarcated from acropodite stem by impression on lateral surface.

Color in Life. — Paranota red; metaterga black, without stripes along caudal margins; collum without stripes along either margin.

Holotype. — Length 48.3 mm, maximum width 11.4 mm, W/L ratio 23.6%, depth/width ratio 58.8%. Segmental widths as follows:

collum	7.7 mm	14th	11.2
2nd	9.1	15th	10.8
3rd	9.8	16th	10.2
4th	10.6	17th	8.9
5th-7th	10.9	18th	6.4
8th-13th	11.4		
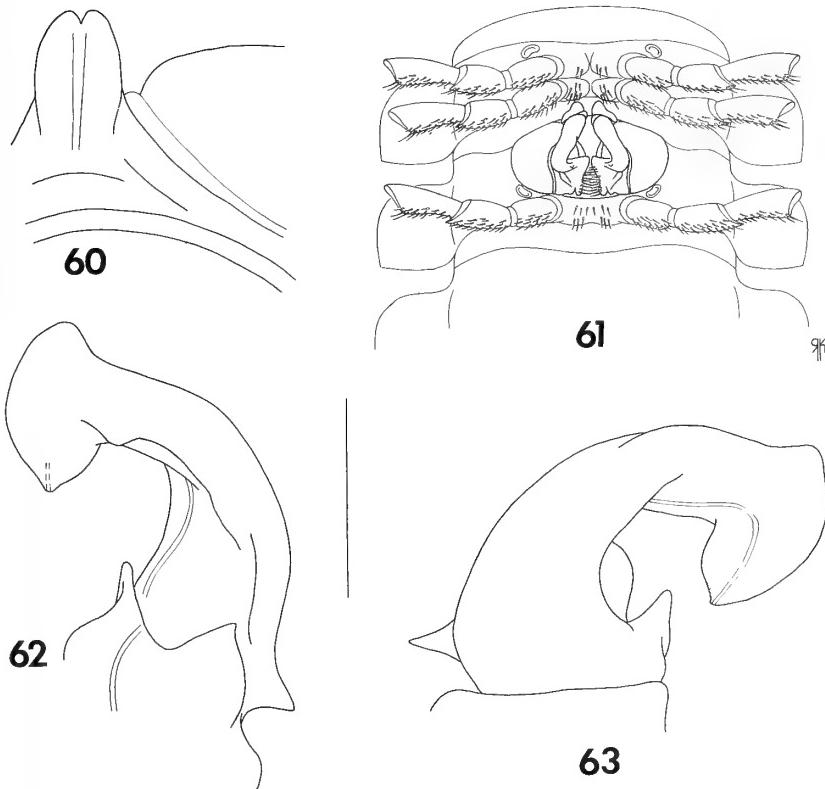
FIGS. 60-63. *Sigmoria (Cleptoria) robusta.* 60, process of 4th sternum of holotype, caudal view. 61, gonopods *in situ,* ventral view of paratype. 62, telopodite of left gonopod of holotype, medial view. 63, the same, lateral view. Scale line for fig. 61 = 1.00 mm; line for other figs. = 1.00 mm for 62-63; 1.33 mm for 60.

Somatic features similar to *l. latior*, with following exceptions:

Width across genal apices 1.5 mm, interantennal isthmus 1.9 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres 2 > 3 > 6 > 4 = 5 > 1 > 7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, genal, and frontal absent, clypeal about 11-11, labral about 16-16.

Terga smooth, polished, becoming coriaceous on paranota. Collum broad, ends extending well below those of adjacent tergite. Paranota moderately depressed, containing slope of dorsum, caudolateral corners rounded through segment 5, blunt on segments 6-11, becoming progressively more acute posteriorly. Peritremata sharp and distinct, strongly elevated above paranotal surface; ozopores located near midlength, opening dorsolaterad.

Sternum of segment 4 with large, apically divided process between 3rd legs, much longer than widths of adjacent coxae (Fig. 60); that of segment 5 with two medially coalesced knobs between 4th legs and longer, more separate projections between 5th legs, latter equal in length to widths of adjacent coxae; sternum of segment 6 without depression on caudal edge, with two rounded, elevated areas between 7th legs, shorter than widths of adjacent coxae. Postgonopodal sterna with two blunt lobes on caudal edge of segment 8 arising from bicruciform impression; segment 9 also with bicruciform impression but flattened between caudal legs; remaining sterna becoming progressively flatter and more plate-like posteriorly, with variably broad, shallow, central impressions. Coxae with low, blunt tubercles arising on segment 9, becoming larger posteriorly; prefemoral spines arising on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.9 mm wide and 2.4 mm long at midpoint, without indentations, sides flush with metazonal surface. Gonopods *in situ* (Fig. 61, of paratype) with acropodites projecting anteriad from aperture, nearly parallel but angling towards each other and extending slightly beyond anterior margin, not overlapping or touching. Gonopod structure as follows (Figs. 62-63): Prefemur with acutely triangular, ventromedial lobe; prefemoral process blunt and narrow, arising from lamina of basal zone, directed toward apical curve. Acropodite massive, heavily sclerotized, forming rectangular arch, overhanging and extending well beyond level of prefemoral process; basal zone broad, with sharply acute spine basally on outer margin, medial surface convex with anterior edge expanded into thin lamina; anterior bend sharp, well defined; peak moderately long and straight, angling slightly ventrad with apex distad; apical curve sharp, well defined; distal zone short and very broad, outer margin not indented, gently rounded and converging with inner to form blunt tip, with short striations on lateral surface; tip directed toward coxae. Medial flange thick, heavy, and narrow, relatively laminate, arising on distal extremity of basal zone, curving across anterior bend and narrowing on proximal part of peak, then expanding into broadly rounded distal lobe, terminating on proximal part of distal zone. Lateral flange lobe-like, located on proximal part of distal zone, produced ventrad, forming highest point of acropodite arch, poorly demarcated from acropodite stem by slight impression in distal zone, continuous with outer margin of distal zone. Prostatic groove crossing to lateral side at anterior bend, curving onto distal zone and opening terminally.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 41.5 mm, maximum width 9.9 mm, W/L ratio 23.9%, depth/width ratio 63.6%. Agreeing closely with males in somatic features, except ends of collum not produced beyond those of following tergite. Cyphopods *in situ* with corner of receptacle and valves visible in aperture, latter directed caudolaterad. Receptacle large, cupped around medial side of valves, with ridges and lobes, surface rugulose. Valves large, equal, surfaces finely granulate.

Variation. — Except for slight changes in the length and shape of the prefemoral process and the spine on the basal zone, the gonopods in this species are essentially uniform. Likewise, all males possess elevated areas on the 6th sternum between the 7th legs and lack a depression at this point.

Ecology. — *Sigmoria (Cleptoria) robusta* occurs under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — The Piedmont Plateau in the western corner of South Carolina between the Toxaway and Chatooga Rivers. The species extends to the base of the Blue Ridge Escarpment but apparently is absent from the mountains. Specimens were examined as follows:

SOUTH CAROLINA. — *Oconee Co.,* 7.1 mi. NE Walhalla, along SC hwy. 24 at Little R., M, 7 May 1977 (NCSM A1557); 4.8 mi. W Seneca, along SC hwy. 13 at Corneross Cr., 2F, 7 May 1977 (NCSM A1554); 5 mi. S Seneca, along SC hwy. 54 at Hartwell Res., 2M, 7 May 1977 (NCSM A1555); 10.8 mi. SW Seneca, along SC hwy. 168, 0.3 mi. S jct. SC hwy. 86, 2M, F, 7 May 1977 (NCSM A1553) TYPE LOCALITY; and 5.7 mi. SE Oakway, along SC hwy. 66 at Beaverdam Cr., M, F, 10 June 1978 (NCSM A2061). *Anderson Co.,* 10.3 mi. SW Pendleton, along SC hwy. 192 at Beaverdam Cr., M, 4F, 7 May 1977 (NCSM A1552).

Remarks. — *Sigmoria (Cleptoria) robusta* shares ancestry with *abbotti* and represents a population that became isolated north of the Savannah River. They are similar in the narrow medial flanges and the expanded, laminate anterior margins of the basal zones that lead into the prefemoral processes. However, the spine on the basal zone is larger in *robusta,* and there is a distinct distal lobe on its medial flange instead of a thickening or boss as in *abbotti.* Another difference obtains on the 6th sternum, which is moderately depressed between the 7th legs in *abbotti* and displays two elevated lobes in *robusta.*

Sigmoria **(Cleptoria) macra** (Chamberlin), new combination   Figs. 64-67

Cleptoria macra Chamberlin, 1939:9, pl. 4, Figs. 36-37. Chamberlin and Hoffman, 1958:28.
    Hoffman, 1967:7-11, Figs. 3, 5, 6, and 12.
Cleptoria rileyi Loomis, 1943:402.

Hoffman (1967) presented a detailed description of *macra,* and his medial gonopodal illustration shows the medial flange arising on the basal zone and terminating on the peak. The flange in *macra* is thus in the same position as those in *shelfordi* and *arcuata* (Shelley 1980a, 1981b) and a close relationship is confirmed by new material with a spur on the outer surface of the acropodite at the anterior bend (Figs. 65-67). This spur is homologous to that in *shelfordi,* leaving no doubt that the species are congeneric. Loomis understood this fauna better than any subsequent author,

as he (1944) assigned *shelfordi* to the same genus as *macra,* and (1943) expressed doubts as to the validity of *Cleptoria.*

Diagnosis. — A large species of *Sigmoria* with medial flange extending between midlength of basal zone and distal extremity of peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral processes short and variably triangular; acropodite moderately thick and heavy, arch either flattened or gently rounded, extending only slightly beyond level of prefemoral process; basal zone moderately long, without modifications; anterior bend broad, poorly defined; peak variable, flattened or gently curved, with or without sharply acute spur on outer surface; apical curve well defined; distal zone short, outer margins slightly indented, directed perpendicularly from peak, sides curving and narrowing to blunt tip; medial flange variable in length and configuration, arising on distal extremity of basal zone, terminating from midlength of peak to proximal portion of distal zone, usually with curved
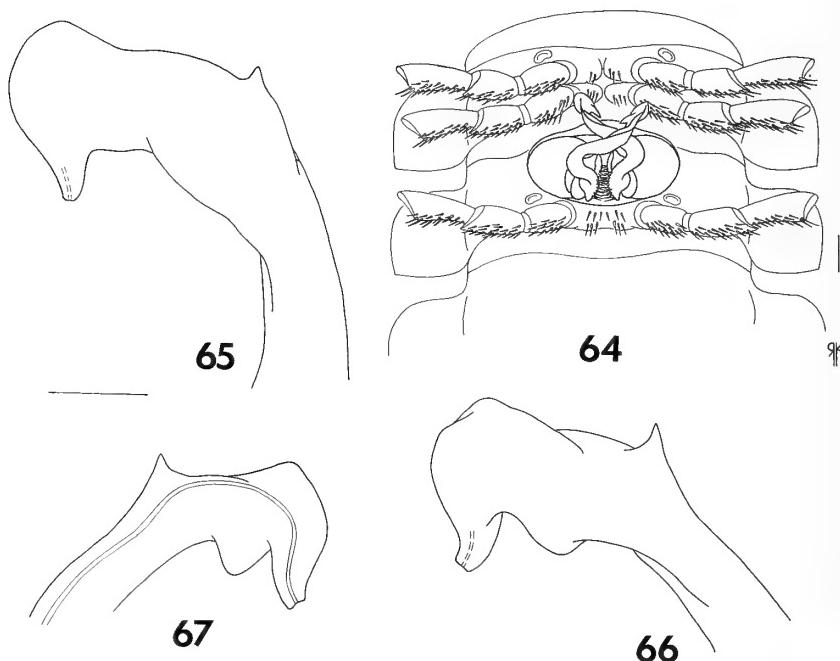
FIGS. 64-67. *Sigmoria (Cleptoria) macra.* 64, gonopods *in situ,* ventral view of male from Newberry Co., SC. 65, acropodite of left gonopod of the same, medial view. 66, distal part of acropodite of male from Greenville Co., SC, medial view. 67, the same, lateral view. Scale line for fig. 64 = 1.00 mm; line for other figs. = 1.00 mm for each.

proximal margin, then indented and terminating in rounded or triangular distal lobe; lateral flange a broadly rounded lobe on proximal part of distal zone, protruding ventrad, demarcated from acropodite stem by slight impression on lateral surface.

Color in Life. — Paranota red; metaterga black, without stripes along caudal edges; collum also without stripes along either margin.

Holotype. — Process of 4th sternum moderately long, equal in length to widths of adjacent coxae (Hoffman 1967, Fig. 3).

Gonopods *in situ* (Fig. 64, not this specimen) with acropodites crossing at midlength in midline of aperture, extending forward over anterior margin to between 7th legs. Gonopod structure as follows (Hoffman 1967, Figs. 65-67): Prefemoral process short, nearly straight, tapering to acuminate tip, directed toward distal zone. Acropodite thick and heavy, well sclerotized, forming broad, rectangular arch, overhanging and extending slightly beyond level of prefemoral process; basal zone moderately long, without modifications; anterior bend sharp, well defined; peak moderately long, broad, and flattened, rising continuously to apex at distal extremity, with thin curved lamella on outer margin of lateral surface; apical curve sharp, well defined, approximately a right angle; distal zone short, with outer edge slightly indented and angling sharply inward to form blunt tip; latter directed toward coxa. Medial flange relatively broad, thin, and laminate arising on distal extremity of basal zone, curving broadly across anterior bend and terminating on distal extremity of peak. Lateral flange lobe-like, located on proximal part of distal zone, broadly rounded and produced ventrad, poorly demarcated from acropodite stem by slight depression in lateral surface. Prostatic groove crossing to lateral side at anterior bend, running along outer margin of peak, curving sharply and extending through center of distal zone to terminal opening.

Variation. — I have collected *macra* five times, all south of the type locality, and each male possesses a short acute spur on the outer margin at the anterior bend, or at midlength of the medial flange (Figs. 65-67). Hoffman (1967) did not mention this feature in his account of variation, but my specimens, collected at nearly the same site in Newberry County possess it (Fig. 66). Northern populations evidently lack the spur and are atypical. Males from the center of the range in Greenville County have broadly rounded, nearly triangular lobes distally on the medial flange (Figs. 66-67).

Distribution. — A linear area approximately 60 miles long in piedmont South Carolina, ranging from north of Greenville to the Saluda River in southern Newberry County. Hoffman (1967) predicted that *macra* would probably be found in North Carolina but I have sampled intensively north of the type locality without encountering it. *Sigmoria (Cleptoria) divergens* Chamberlin is common in this area and along the North Carolina-South Carolina state line in the Blue Ridge escarpment. As with *simplex (Croatania),* the type locality is near the northern range limit. Material was examined from the following new localities:

SOUTH CAROLINA. — *Greenville Co.,* 8.7 mi. SW Fountain Inn, along SC hwy. 68 at Reedy Cr., M, 3F, 11 June 1978 (NCSM A2069); and 12.5 mi. SW Fountain Inn, along SC

hwy. 51 at Mountain Cr., M, 11 June 1978 (NCSM A2068). *Newberry Co.,* 5.2 mi. N Chappells, along SC hwy. 56, 0.2 mi. N jct. SC hwy. 347, 4M, 2F, 3 May 1977 (NCSM A1523) and M, F, 22 April 1982 (NCSM A3927).

Sigmoria (Cleptoria) shelfordi (Loomis), new combination

Cleptoria shelfordi Loomis, 1944:172-173, Fig. 4. Chamberlin and Hoffman, 1958:28.
Brevigonus shelfordi: Shelley, 1980a:35-41, Figs. 1-13; 1981b:55-56.

Occurring along the northern side of the Savannah River in piedmont South Carolina (McCormick, Abbeville and Oconee counties), *shelfordi* was adequately described in two previous papers (Shelley 1980a, 1981b), the latter characterizing the gonopods in "sigmoid" terminology. Aspects of variation, ecology, and distribution were also discussed. No new records are available.

In the first account (Shelley 1980a) two gonopodal variants were described. Variant A has a basal spine on the outer surface of the basal zone, a large medial flange that partly or completely obscures the acropodite stem in medial view, and a compact curvature with the tip directed toward the coxa. It usually lacks the spur, and the stem is apically entire. Variant B lacks the basal spine, has a narrower medial flange that reveals the prostatic groove to the crossover point, and has a more open curvature with the tip directed generally parallel to the coxa. This form, which includes the type specimens, possesses the spur and is usually apically indented. Occasionally, characters from one form appear in the other (i.e. the spur of B in A, and the apical configuration of A in B), proving that they are not reproductively isolated. Subspecific recognition is also not justified because they occur sympatrically and are interspersed throughout the range. Therefore, *shelfordi* is a polymorphic species. Although the two variants are intermixed in McCormick and Abbeville counties, form A tends to occur more in the west proximal to the ranges of *arcuata* and *robusta,* and form B more in the east and north proximal to *macra.* In form B, absence of the basal spine is shared with *macra,* and presence of a spur is shared with southern populations of *macra.* Since *shelfordi* and *macra* are proximal and lack known intergrades, they are considered separate species even though geographic variation in these features crosses cladistic lines.

I return to *shelfordi* the Oconee County record [Clemson vic., under dead pig, 2M, F, 18 July 1962, J.A. Payne (RLH)], which I (1980a) assigned to it and later (1981b) switched to *arcuata.* This record is troublesome because it is segregated by the range of *arcuata.* The form lacks a prefemoral process and has a stronger basal spine, a broader medial flange, and greater acropodal curvature than the other males of *shelfordi.* The Oconee County

population, parapatric with *robusta,* agrees with *arcuata* in lacking a prefemoral process, but despite proximity, this is best considered convergence.

Diagnosis. — A large species of *Sigmoria* with medial flange extending between proximal part of basal zone and distal extremity of peak and with red paranota, metaterga without stripes; gonopods with following diagnostic characters: prefemoral process present or absent, variable; acropodite heavily sclerotized, arch extending only slightly beyond level of prefemoral process; basal zone relatively long, about 2/3 of acropodite length, with or without variable basal spine on outer edge; anterior bend variable; peak about 1/3 of acropodite length, flattened or gently curved, with or without short, acute spur on outer or medial surfaces; apical curve and distal zone absent, acropodite terminating in blunt inner corner of peak, apical edge variable; medial flange thick but laminate, length and configuration variable; lateral flange absent.

Color in Life. — Metaterga red; paranota black without stripes along caudal edges; collum with or without narrow stripe along anterior margin.
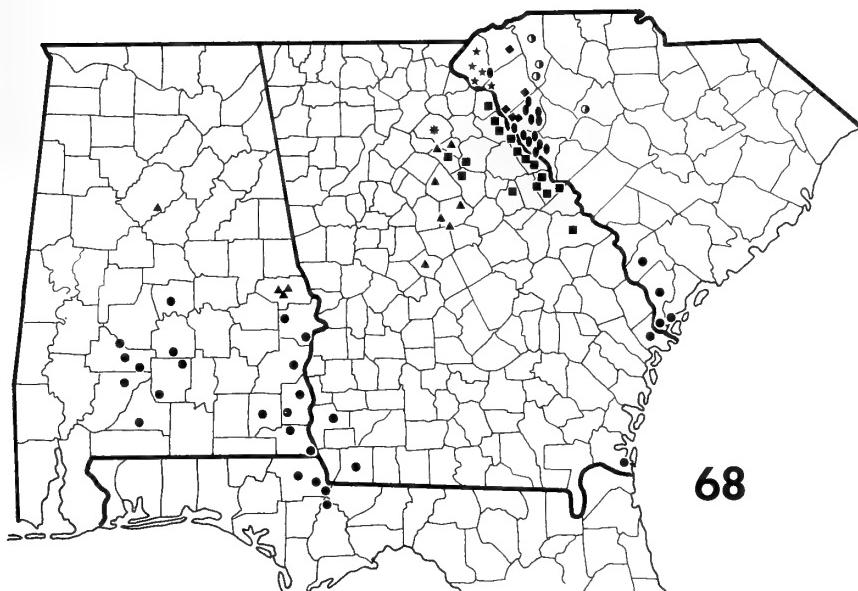
Fig. 68.   Distributions of *australis* and the subgenus *Cleptoria* in the southeastern states. Dots, *australis;* triangles, *rileyi;* squares, *abbotti;* asterisk, *bipraesidens;* stars, *robusta;* diamonds, *arcuata;* ovals, *shelfordi;* half shaded dots, *macra.*

Sigmoria (Cleptoria) arcuata (Shelley), new combination

Brevigonus arcuatus Shelley, 1981b:56-60, Figs. 1-5.

Sigmoria (Cleptoria) arcuata occurs in the Savannah River Valley between the Oconee County locality and all others of *shelfordi*. It ranges northward into Pickens County near the Blue Ridge Front. The previous paper (Shelley 1981b) described *arcuata* in detail and discussed variation, ecology, and distribution. Since no new records are available, I present here only a diagnosis and color statement.

Diagnosis. — A large species of *Sigmoria* with medial flange usually extending between proximal part of basal zone and midlength of peak and with red paranota, metaterga without markings; gonopods with following diagnostic characters: prefemoral process absent; acropodite moderately thick, arch a broad curve extending beyond level of prefemur; basal zone with prominent acute spine basally on caudal edge, length variable; anterior bend variable; peak gently curved or flattened; apical curve poorly defined; distal zone moderately long, curving broadly into arch, narrowing smoothly and continuously distally, tip simple or reflexed; medial flange with variable tooth on slightly wider proximal part, then narrowing and either terminating by blending into outer margin of peak or widening again and terminating abruptly at midlength of peak; lateral flange laminate, located on apical curve and proximal part of distal zone.

Color in Life. — Paranota red; metaterga dark glossy black, without stripes along caudal edges; collum also without stripes along either margin.

SIGMORIA (CHEIROPUS) Loomis, new status

Cheiropus Loomis, 1944:170-171. Chamberlin and Hoffman, 1958:25. Jeekel, 1971:253. Hoffman, 1979:159. Shelley 1984a:265-267.
Stelgipus Loomis, 1944:173. Jeekel, 1971:288. Hoffman, 1979:159.
Fontaria: Chamberlin and Hoffman, 1958:33.
Lyrranea Hoffman, 1963:114-115; 1979:159.
Prionogonus Shelley, 1982:460-462. **NEW SYNONYMY.**

Types species. — Of *Cheiropus, C. plancus* Loomis, 1944, by original designation; of *Stelgipus, S. agrestis* Loomis, 1944, by original designation; of *Lyrranea, L. persica* Hoffman, 1963, by original designation; of *Prionogonus, P. haerens* Shelley, 1982, by original designation.

Diagnosis. — Paranota usually red, occasionally orange, metaterga usually with concolorous stripes connecting paranotal markings, rarely uniformly black; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture and inserting between 7th legs; prefemoral

process present or absent, moderate when present; acropodites moderately thick and heavy, occasionally massive, well sclerotized, oriented normally on coxa with inner surface directed anteriomediad; basal zone with or without row of spurs on outer surface, occasionally extending onto peak, otherwise unmodified; medial flange present or absent, variable but usually broad and dilated, laminate to thickened, located on peak or distal part of acropodite in forms lacking distal zone; lateral flange present or absent, laminate; distal zone curving either strongly laterad and obscured in medial view by acropodite stem or medial flanges, or replaced by variably positioned solenomerite, latter best revealed in lateral view; tip variable.

Remarks. — The subgenus *Cheiropus,* containing the southernmost apheloriine species, is united chiefly by the laterally directed distal zone or its solenomerite substitute. It lacks geographic cohesion and is divided into four species groups.

The *Australis* group

The *australis* group contains a relatively undifferentiated species in the Coastal Plains of South Carolina, Georgia, Alabama, and Florida. It occurs in three allopatric populations that have not diverged and are unquestionably conspecific.

Component. — *australis,* new species

Sigmoria (Cheiropus) australis Shelley, new species   Figs. 69-72

Type specimens. — Male holotype (NCSM A2874) and three male and two female paratypes collected by R.M. Shelley and P.T. Hertl, 15 September 1979, from Torreya State Park, Liberty Co., FL. The lushness of this park makes it a popular arthropod collecting site and *australis* has been taken there many times. Too numerous to be cited with complete data, additional paratypes of both sexes are available in the NCSM, FSCA, and WAS.

Diagnosis. — A moderate to large species of *Sigmoria* with medial flange extending between distal extremities of basal zone and peak and with red paranota and variable metaterga, with or without red transverse stripes; gonopods with following diagnostic characters: acropodite moderately thick, arch in form of inverted L, extending slightly beyond level of prefemoral process; basal zone relatively long; anterior bend and apical curve well defined, latter forming arc with narrow diameter, peak short,

gently curved; distal zone short, curving laterad from peak, not coplanar with other sections, obscured in medial view by medial flange, sides narrowing to acuminate tip; medial flange relatively long, widening into triangular lamina on distal extremity of peak then terminating abruptly; lateral flange narrow and inconspicuous, located on distal extremity of peak.

Color in Life. — Paranota red; metaterga black, with or without concolorous red stripes along caudal edges connecting paranotal markings; collum with or without red stripes along both margins.
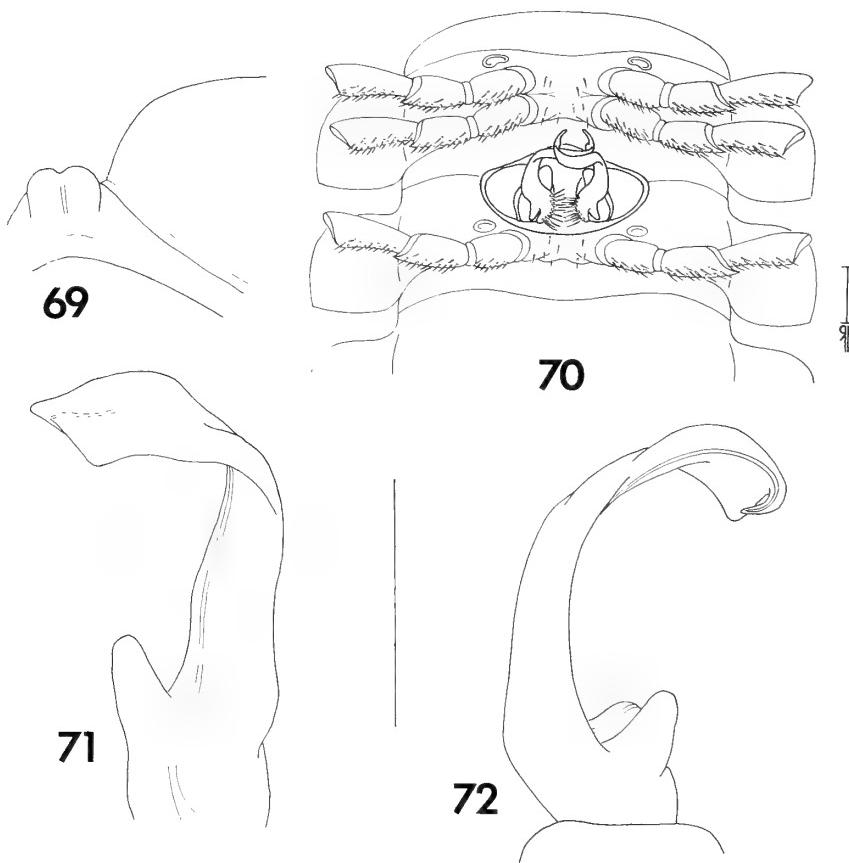
FIGS. 69-72. *Sigmoria (Cheiropus) australis.* 69, process of 4th sternum of holotype, caudal view. 70, gonopods *in situ,* ventral view of male from Camden Co., GA. 71, telopodite of left gonopod of holotype, medial view. 72, the same lateral view. Scale line for fig. 70 = 1.00 mm; line for other figs. = 1.00 mm for 71-72, 1.33 mm for 69.

Holotype. — Length 47.3 mm, maximum width 12.8 mm, W/L ratio 27.1%, depth/width ratio 56.3%. Segmental widths as follows:

collum	7.9 mm	7th	12.6
2nd	8.5	8th-14th	12.8
3rd	9.5	15th	12.0
4th	11.0	16th	11.2
5th	12.0	17th	9.7
6th	12.3	18th	6.8

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.1 mm, interantennal isthmus 1.8 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 8-8, labral 14-14.

Dorsum appearing smooth and polished, but moderately coriaceous. Collum broad, ends extending well below those of following tergite. Paranota relatively flat, interrupting slope of dorsum and subparallel to substrate, caudolateral corners rounded through segment 4, blunt on 5-8, becoming progressively more acute posteriorly. Peritremata distinct, sharply elevated above paranotal surface; ozopores located near middle of peritremata, opening dorsolaterad.

Sternum of segment 4 with small process, barely elevated above sternal surface, much shorter than widths of adjacent coxae (Fig. 69); that of segment 5 with two low paramedial knobs between anterior legs and slightly elevated flattened areas between caudal legs; 6th sternum with only slight depression between 7th legs, these set slightly farther apart than 6th legs. Postgonopodal sterna flattened and plate-like, with shallow transverse grooves between leg pairs on segments 8-12 and variably broad, shallow, central impressions on remaining segments. Coxae with low, rounded tubercles beginning on segment 10; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.1 mm wide and 1.3 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 70, not this specimen), with acropodites projecting ventrad from aperture, bending laterad and extending over opposite side in front of and behind each other, curving anteriad with one behind overlapping other and one in front extending slightly beyond anterior margin. Gonopod structure as follows (Figs. 71-72): Prefemoral process short, blunt, directed toward distal zone. Acropodite moderately thick, forming inverted L shaped arch, overhanging and extending slightly beyond level of prefemoral process; basal zone relatively long, unmodified; anterior bend sharp, well defined; peak relatively short, gently curved; apical curve relatively sharp, well defined, forming arc with very narrow diameter; distal zone short, curving laterad from peak, not coplanar with other regions, obscured in medial view by medial flange; tip acuminate. Medial flange arising on distal extremity of basal zone, widening into triangular lamina on distal extremity of peak and terminating abruptly thereafter. Lateral flange a short, narrow, inconspicuous lamella on peak opposite trianglar part of medial flange. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

Male Paratypes. — Some male paratypes have more acuminate prefemoral processes, but otherwise all agree closely with the holotype.

Female Paratype. — Length 42.9 mm, maximum width 11.8 mm, W/L ratio 27.5%, depth/width ratio 62.7%. Cyphopods *in situ* with edge of receptacles and opening of valves visible in aperture. Receptacle moderate, situated on medial sides of valves, with ridge on this side, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — Aside from minor changes in the length and bluntness of the prefemoral process and the breadth of the medial flange, the gonopods of *australis* are quite constant throughout the range. Size and color pattern vary, however, and as noted under "Color in Life," individuals may or may not have red stripes along the caudal margins of the metaterga and collum. The types and the sample from Decatur County, Georgia, lack stripes, but as far as one can tell from faded preserved specimens, all others possess them. All the individuals I collected in Alabama, Georgia, and South Carolina were striped.

Regarding size, the types are near maximum for the species. The opposite extreme is found along the Atlantic Coast, as shown by a male from Beaufort County, South Carolina, which measures 29.1 mm in length, 7.4 mm in width, W/L ratio 25.4%, depth/width ratio 53.4%. Large males appear extremely broad in dorsal view, but this is an illusion created by the unusually flat paranota. This effect is less noticeable in small individuals.

Ecology. — *Sigmoria (Cheiropus) australis* occurs in a variety of mesic deciduous forests under thin layers of leaves on relatively hard substrates, preferably near water sources. In Crooked River State Park, Camden County, Georgia, I found *australis* on sandy-humus soil in a live oak-magnolia forest, but it was absent from the litter of these species occurring instead under other hardwoods. It occurs syntopically with *serrata* at this site, but they are dominant at different times of the year (Shelley 1984a). *Sigmoria (Cheiropus) australis* was more abundant in July 1977 but was absent in October 1980, when *serrata* was present. The life histories therefore seem to be adjusted to minimize ecological competition. A comparable situation may exist in western Georgia at Kolomoki Mounds State Park, Early County, where *australis* and *Dynoria medialis* Chamberlin occur syntopically in typical climax piedmont forest. I have visited this locality twice and found them to be equally abundant in November 1977, whereas *D. medialis* was more common in May 1983.

Distribution. — The Coastal Plains of Alabama, Georgia, southern South Carolina, and northern Florida, ranging from near the Alabama River to the Atlantic Ocean and extending inland to the edge of the Fall Zone, just crossing the Alabama River northwest of Montgomery. The distribution spans several large rivers including the Chattahoochee, Altamaha, and Savannah, but *australis* has not been encountered south of the St. Marys River in Nassau or Duval counties, Florida. As shown in Fig. 68 the available material clusters into three disjunct areas — the Atlantic coast from Hampton County, South Carolina, to Camden County, Georgia; along both sides of the Chattahoochee River from the inner Coastal Plain of Russell County, Alabama, to Liberty County, Florida; and in central Alabama from Autauga to Conecuh counties. There are no

anatomical differences between these groups, however, and all are unquestionably conspecific. Additional collecting may eventually connect the two areas in Alabama, but I doubt if the Chattahoochee and Atlantic Coastal populations will ever be connected. Specimens were examined as follows:

ALABAMA: *Autauga Co.,* 2.5 mi. SE Prattville, M, F, 20 August 1960, L. Hubricht (RLH). *Lowndes Co.,* 3 mi. E Braggs, 2F, 4 July 1960, L. Hubricht (RLH). *Wilcox Co.,* along AL hwy. 41, 2.5 mi. S Dallas Co. line, 2M, F, 22 May 1980 (NCSM A3124); 3.5 mi. N Camden, 2M, 11 November 1962, L. Hubricht (RLH); and 2 mi. S Oak Hill, M, 10 May 1960, L. Hubricht (RLH). *Butler Co.,* 3 mi. SE Searcy, 6M, 5F, 9 April 1960, L. Hubricht (RLH); 9.8 mi. NE Greenville, along US hwy. 31 at Pigeon Cr., F, 2 juvs., 21 April 1983 (NCSM A4039); and 3 mi. NW McKenzie, along US hwy. 31, 2M, 2F, 9 April 1960, L. Hubricht (RLH). *Monroe Co.,* 12 mi. NNE Monroeville, along AL hwy. 21, 4.9 mi. N jct. AL hwy. 265, M, 22 April 1983 (NCSM A4046). *Conecuh Co.,* 2.2 mi. SW Evergreen, 10M, 10F, 26 June 1961, L. Hubricht (RLH). *Russell Co.,* 3 mi. N Uchee, 4M, 2F, 12 June 1960, L. Hubricht (RLH); and 14.9 mi. S. Phenix City, along AL hwy. 165, 0.3 mi. N jct. AL hwy. 38, 2F, 26 April 1983 (NCSM A4064). *Barbour Co.,* 13 mi. E Clayton, M, F, 5 September 1959, L. Hubricht (RLH) and 2.7 mi. S Eufaula, along US hwy. 431, 0.5 mi. S jct. AL hwy. 30, F, 29 April 1983 (NCSM A4067). *Henry Co.,* 5 mi. W Capps, M, 6 August 1960, L. Hubricht (RLH) and 2.8 mi. NE Abbeville, along AL hwy. 47, 2.1 mi. E jct. AL hwy. 95, 2F, 29 April 1983 (NCSM A4069). *Dale Co.,* 5.6 mi. NE Ozark, along AL hwy. 105 at Judy Cr., M, 29 April 1983, (NCSM A4071). *Houston Co.,* 4 mi. E Webb, 2F, 9 July 1967, D.R. Whitehead (RLH) and Chattahoochee St. Pk., 4M, 3F, 30 April 1983 (NCSM A4080).

FLORIDA: *Jackson Co,* 5.7 mi. W Greenwood, M, 11 July 1973, R.M. Blaney (FSCA); Florida Caverns St. Pk., several males and females taken in April, May, June, and July from 1957-1975 by various collectors (FSCA, WAS); Marianna, males and females collected from 1961-1970 by various persons (FSCA); Three Rivers St. Pk, 8M, 5F, 19 July 1953, W.A. Shear (WAS); and 3.3 mi. E Sneads, along Appalachicola R., 3M, 2F, 7 September 1959, L. Hubricht (RLH). *Liberty Co.,* Torreya St. Pk., 4M, 2F, 15 September 1979 (NCSM A2874) and several other males and females taken from March-October from 1968-1977 by various collectors (NCSM, FSCA, WAS) TYPE LOCALITY.

GEORGIA: *Early Co.,* Kolomoki Mounds St. Pk., 2M, 19 November 1977 (NCSM A1783) and M, 1 May 1983 (NCSM A4023). *Decatur Co.,* 1.4 mi. W Climax, 2M, F, 7 September 1959, L. Hubricht (RLH). *Camden Co.,* Crooked River St. Pk., 3M, 8F, 3 July 1977 (A1605) and M, 2 October 1980 (NCSM A3590). *Chatham Co.,* 1.7 mi. E Silk Hope, 2M, 12 September 1959, L. Hubright (RLH).

SOUTH CAROLINA: *Hampton Co.,* 0.8 mi. SE Hampton, M, 19 September 1959, L. Hubricht (RLH). *Beaufort Co.,* 2.5 mi. W. Bluffton, along SC hwy. 46, M, 12 September 1980 (NCSM A3507). *Jasper Co.,* 7 mi. S Hardeeville, M, 19 September 1959, L. Hubricht (RLH); and Ridgeland, M, 28 March 1975, D. Brody (AMNH).

Remarks. — *Sigmoria (Cheiropus) australis* has been reported twice before (Shelley 1979a, 1984a), first as representing an undiagnosed apherloriine genus and secondly as an undescribed species of *Hubroria*. I once thought *australis* related to species in the Cumberland Plateau of Tennessee for which the name *Hubroria* is available. Since the medial flange is broadest distad and the distal zone curves laterad from the peak, *australis* does conform in these traits to the Cumberland species. I therefore have

spent days searching for *Sigmorias* from Jackson and Marshall counties to Birmingham, and since these efforts were unproductive, I do not think that the Cumberland fauna occurs south of the Tennessee River. Except for the medial flanges there is little similarity between the gonopods of *australis* and those of any Cumberland species as there would be in the case of a direct relationship. Only after revising *Cheiropus* (Shelley 1984a) did the affinity of *australis* for *stibarophalla* become evident. The latter, in the eastern Blue Ridge Mountains of North Carolina, is some 200 miles northwest of the closest known locality of *australis* in South Carolina. The region between *stibarophalla* and *australis* is occupied by more divergent forms of *Cheiropus*. Like *stibarophalla, australis* has a short prefemoral process, a sharp apical curve forming an arc with very narrow diameter, a short distal zone that curves laterad from the peak, and a medial flange that arises at the anterior bend and terminates at the apical curve, obscuring the distal zone in medial view. The similarities between their gonopods is evident by comparing Figs. 71-72 with Figs. 25-26 in Shelley (1981a).

Of nearly equal interest to the relationship with the allopatric *stibarophalla* are the allopatric populations of *australis* (Fig. 68). The two Alabama areas may eventually be joined by further collecting, but I doubt that the middle one will ever be connected with the eastern. There is no anatomical divergence and the forms in all three areas vary within similar limits.

The *Divergens* Group

The *divergens* group was proposed by Shelley (1983a) for a single species, but it is now enlarged to accommodate two species in the eastern Blue Ridge Mountains of the Carolinas. The distal zones curve strongly laterad from the peak but maintain their identities as distinct acropodal regions. Details are presented in Shelley (1981a, 1983a).

Components. — divergens Chamberlin, *stibarophalla* Shelley

The *Haerens* Group

In this and the following group, the distal zone is indistinguishable as a separate acropodal region and is represented instead by a solenomerite that is best viewed in lateral perspective. In the *haerens* group, the structure is located terminally on the distal extremity of the peak, perpendicular to the acropodal axis in two species and coaxial in one. The three included species, previously placed in the genus *Prionogonus,* were discussed in detail by

Shelley (1982). They are united by a synapomorphy, the row of spurs along the basal zone.

Components. — *haerens* (Shelley), *divaricata* (Shelley), *thrinax* (Shelley).

The *Planca* Group

The *planca* group contains the southernmost species in *Sigmoria,* which were formerly the sole components of the genus *Cheiropus* (Shelley 1984a). Here the solenomerite occurs at different positions on the acropodite stem, but always proximal to the tip. The basal zones are unmodified. The acropodite of *agrestis* displays a sigmoid curvature, which is absent in the curvilinear species *planca* and *serrata*. The peak is also greatly enlarged and thickened in these three species and often possesses marginal dentations. The fourth species, *persica,* is highly modified with the solenomerite arising basally from the acropodite. Further details are available in Shelley (1984a).

Components. — *planca* (Loomis), *agrestis* (Loomis), *persica* (Hoffman), *serrata* (Shelley)

Additional Record. — *serrata* — GA, Camden Co., Cumberland Island, M, 5 July 1984 (NCSM A4223).

SIGMORIA (SIGIRIA) Chamberlin, new status

Sigiria Chamberlin, 1939:9. Chamberlin and Hoffman, 1958:48. Jeekel, 1971:287.

Type species. — *Sigiria scorpio* Chamberlin, 1939 [= *Sigmoria rubromarginata* (Bollman)], by original designation.

Diagnosis. — Paranota yellow, red or violet/purple, metaterga with concolorous stripes connecting paranotal markings; gonopods *in situ* with acropodites extending well beyond anterior margin of aperture and inserting between 7th legs; prefemoral process moderate; acropodites thin and fragile to moderately thick and heavy, oriented normally on coxa with inner surface directed anteriomediad; basal zone without modifications; medial flange present, laminate, location varying from proximal portion of peak to distal zone, lateral flange usually present, variably laminate; distal zone variable but usually more or less coplanar with basal zone.

Remarks. — *Sigiria* is revived from synonymy under *Sigmoria* for a heterogeneous assemblage in the southern Appalachians with concolorous paranota and metatergal stripes. The acropodites are highly variable but tend to connect through a spectrum of intermediate forms. Two species groups are recognized partly on the basis of geography, and partly on color.

The *Rubromarginata* Group

The *rubromarginata* group includes forms previously in this group, the *nigrimontis* and *inornata* [= *simplex* (Shelley 1981a)] groups, plus a new species on the Blue Ridge escarpment of Virginia. All except the last have red paranota and red metatergal stripes, this species being yellow. The acropodites are highly variable, but the extremes tend to join through forms of *nigrimontis intermedia,* which is appropriately named. The species-group name of *simplex* (Shelley 1981a) is changed to avoid homonymy with *simplex* Shelley (1977), and the former eastern race of *rubromarginata,* which is continuous with intergrades on the Blue Ridge Front, is elevated to specific status. Its range is isolated from *rubromarginata* by around 30 miles, and anatomical divergence has occurred.

Components. — *rubromarginata* (Bollman); *austrimontis* Shelley; *whiteheadi,* new species; *nigrimontis n. nigrimontis* (Chamberlin), *n. intermedia* (Hoffman), *n. angulosa* Shelley, *n. unicoi* (Shelley); *inornata, new* name; *truncata* Shelley; *sigirioides* Shelley.

Sigmoria (Sigiria) austrimontis Shelley, new status

Sigmoria rubromarginata austrimontis Shelley, 1981a:102-103, Figs. 100-103.

Under this binomial I include the homogeneous population in the South Mountains of North Carolina and the contiguous, heterogeneous assemblage of forms anatomically intermediate between it and *rubromarginata* occurring in the Blue Ridge escarpment and western piedmont lowlands. Genetic interchange with *rubromarginata* is no longer possible, as the ranges are now disjunct, and as stated in the introduction, such populations are now recognized at the specific level. This situation is clearly one where a formerly continuous range, with localized gene pools in the peripheries and intergrade forms in an intermediate geographical position, underwent vicariance partitioning.

Sigmoria (Sigiria) whiteheadi Shelley, new species   Figs. 73-76

Type specimens. — Male holotype and two female paratypes (RLH) collected by R.L. Hoffman, 20 May 1983, from Patrick Co., VA, along Laurel Creek on Blue Ridge parkway at mile 174.3. Male paratype (RLH) taken by same collector at same locality, 23 June 1984.

Diagnosis. — A small species of *Sigmoria* with medial flange on peak and with yellow paranota and yellow metatergal stripes; gonopods with following diagnostic characters: prefemoral process short, blunt;

acropodite moderately thick and heavy, curvature forming narrow arc; peak short and gently curved; distal zone curving laterad from peak, not coplanar with basal zone, bent sharply inward into arch at midlength; medial flange thin and narrow, margin linear, poorly demarcated from acropodite stem; lateral flange located opposite medial, flared outward proximad.

Color in Life. — Paranota bright lemon yellow; metaterga black with concolorous yellow stripes along caudal margins connecting paranotal markings; collum with yellow stripes along both anterior and posterior edges.
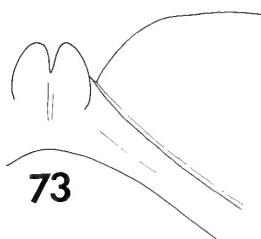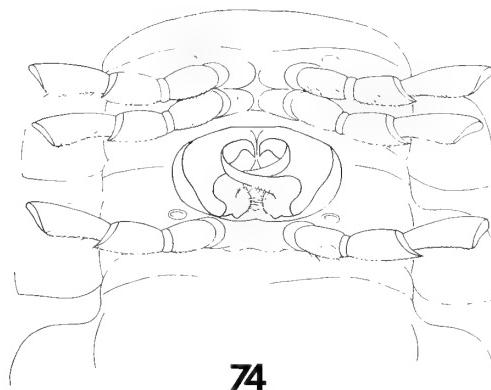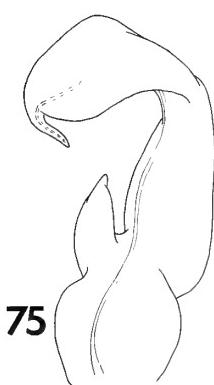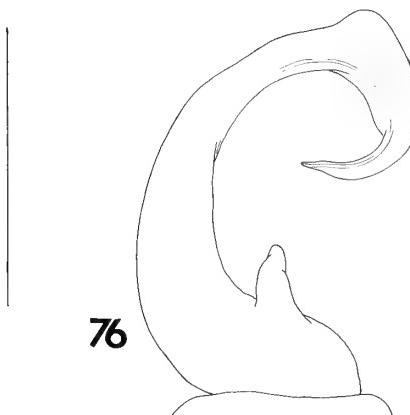
FIGS. 73-76. *Sigmoria (Sigiria) whiteheadi.* 73, process of 4th sternum of holotype, caudal view. 74, gonopods *in situ,* ventral view of holotype. 75, telopodite of left gonopod of the same, medial view. 76, the same, lateral view. Scale line for fig. 74 = 1.00 mm; line for other figs. = 1.00 mm for 73 and 76; 1.25 mm for 75.

Holotype. — Length 31.1 mm, maximum width 6.9 mm, W/L ratio 22.2%, depth/width ratio 62.3%. Segmental widths as follows:

collum	5.1 mm	15th	6.5
2nd	6.1	16th	6.2
3rd	6.5	17th	5.5
4th	6.7	18th	4.4
5th-14th	6.9		

Somatic features similar to those of *l. latior,* with following exceptions:

Width across genal apices 3.7 mm, interantennal isthmus 1.1 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2 > 3 > 4 = 6 > 5 > 1 > 7. Genae with trace of central impressions. Facial setae as follows: epicranial 2-2, interantennal absent, frontal 1-1, genal 3-3, clypeal about 8-8, labral about 14-14.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, ends broadly rounded and extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 9, blunt on 10-15, and more acute caudally. Peritremata relatively flat, faintly elevated above paranotal surface. Ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum small, divided, much shorter than widths of adjacent coxae (Fig. 73); 5th sternum with low paramedian knobs between 4th legs and flattened, elevated areas between 5th, both much shorter than widths of adjacent coxae; 6th sternum with slight recession between caudal legs to accommodate apical curvatures of acropodites. Postgonopodal sterna elevated above stricture, flattened, with bicruciform impressions on 8-9 and variably broad, shallow central depressions thereafter. Coxae without tubercles; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 2.6 mm wide and 1.4 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 74) with acropodites projecting anteriomediad from aperture, overlapping in midline and curving dorsad over opposite side, extending only slightly beyond anterior margin. Gonopod structure as follows (Figs. 75-76): Prefemoral process short, blunt, directed toward peak. Acropodite moderately thick and heavy, well sclerotized, tightly curved forming narrow arch, overhanging and extending well beyond level of prefemoral process; basal zone relatively long, widest basally; anterior bend sharp, well defined; peak short and gently curved; apical curve broad, poorly defined; distal zone moderately long, curving slightly laterad from peak and not coplanar with basal zone, bent abruptly (90°) inward into center of arch at midlength or termination point of flanges, relatively straight distal to bend with sides narrowing smoothly and continuously to acuminate tip; latter directed toward basal zone. Medial flange thin and narrow, arising imperceptibly on proximal part of peak but terminating clearly at midlength of distal zone, margin curving distad. Lateral flange larger than and located opposite medial, arising on distal extremity of peak, terminating at midlength of distal zone, flared outward proximad, margin linear thereafter. Prostatic groove crossing to lateral surface at anterior bend, continuing to terminal opening.

Female paratype. — Length 31.8 mm, maximum width 7.7 mm, W/L ratio 24.2%, depth/width ratio 65.0%. Cyphopods *in situ* with corners of receptacles visible in apertures, valves directed dorsolaterad. Receptacle large, cupped over ventral corners of valves, surface rugulose. Valves moderate in size, subequal, surfaces finely granulate.

Male paratype. — The male paratype agrees with the holotype in all details.

Ecology. — Dr. Hoffman discovered the type specimens in rhododendron litter in a rhododendron/red maple woods. Since this spot is along a

creek, *whiteheadi* seems to be a cove species. It is only the second one found in rhododendron leaves, the other being *truncata* (Shelley 1981a). Others occur near rhododendron, but always in litter of associated hardwood species, usually red maple or dogwood. A male of *l. latior (Sigmoria)* was collected only a foot or so from the male paratype.

Distribution. — Known only from the type locality.

Remarks. — The closest collection of the *rubromarginata* group to *whiteheadi* is Morganton, North Carolina, approximately 120 miles SSW, where *austrimontis* occurs. The acropodite of *whiteheadi* is thicker and heavier than that of *austrimontis,* but in both the distal zones are twisted approximately 90° mediad revealing the faces of the medial and lateral flanges in medial view. However, the apical curve is narrower than in *austrimontis,* forming an arc of shorter diameter, and the distal zone distal to the flanges curves more strongly into the acropodite arch. Thus, the distal half of the distal zone, which is longer than in *austrimontis,* is partly obscured in medial view by the flanges. The prefemoral process is also longer than in *austrimontis* and is not bifurcate.

Sigmoria (Sigiria) inornata Shelley, new name

Sigmoria simplex Shelley, 1981a:45-49, Figs. 29-34.

Sigmoria (Sigiria) inornata is proposed as a new name for this species to avert homonymy resulting from the inclusion of *Croatania* in *Sigmoria* and the resultant transferral of *C. simplex* Shelley, 1977. Priority for the species-group name is with the transferred species.

The *Stenogon* Group

As presently conceived, the *stenogon* group is markedly different in composition from that in its original proposal (Shelley 1981a). One species, *nantahalae (Falloria),* is now in another subgenus, and two species have been added that were previously in the *latior* and *nigrimontis* groups. the gonopods of the three species of the *stenogon* group appear dissimilar in medial view, but considerable conformity is apparent in lateral perspective (compare Figs. 22, 60, and 130 in Shelley (1981a)). The color varies from yellow in the north through red in the central part of the group's range to purple or violet in the south.

Components. — *stenogon* Chamberlin, *areolata* Shelley, *disjuncta* Shelley.

SIGMORIA (FALLORIA) Hoffman, new status

Falloria Hoffman, 1948:93-94. Chamberlin and Hoffman, 1958:33. Jeekel, 1971:264. Hoff-
    man, 1979:159.
Hubroria Keeton, 1960:42. Hoffman, 1979:159. **NEW SYNONYMY.**

Type species. — Of *Falloria, Apheloria bidens* Causey, 1942, by original
designation; of *Hubroria, H. picapa* Keeton, 1960, by original designation.

Diagnosis. — Paranota usually red, occasionally white or light yellow,
metaterga with contrasting stripes, usually blue, connecting paranotal
markings except when latter white or light yellow; gonopods *in situ* with
acropodites extending well beyond anterior margin or aperture and insert-
ing between 7th legs; prefemoral process highly variable, deeply or apically
divided, long and basally globose or moderate or short; acropodites usually
moderately thick and heavy, oriented normally on coxa with inner surface
directed anteriomediad or with inner surface directed mediad; basal zone
usually without modifications, occasionally with dense tubercles; medial
flange usually present and laminate, location varying from basal to distal
zones; lateral flange present or absent, variably laminate; distal zone
variable, either coplanar with basal zone or directed strongly laterad and
nearly coplanar with peak.

Remarks. — *Falloria* is revived from synonymy under *Sigmoria* as the
oldest available name for the heterogeneous assemblage with largely con-
trasting paranotal and metatergal colors in the western part of the generic
range. The acropodites are highly variable, and eight species groups are
recognized.

The *Nantahalae* Group

The *nantahalae* group contains only the single species, which is unique to
the subgenus in the red/white coloration, the absence of a medial flange,
and the presence of a tooth. Further details are available in accounts by
Hoffman (1958a) and Shelley (1981a).

Component. — *nantahalae* Hoffman.

The *Leucostriata* Group

The *leucostriata* group is characterized by a greatly reduced medial flange
on the proximal part of the peak, small medial and lateral lobes opposing
each other proximally on the distal zone, and a curved or bent distal zone

which extends into the arch. It consists of two allopatric species in the western fringe of the Blue Ridge Province in Tennessee and north Georgia. One, *leucostriata,* is the only member of the subgenus with concolorous paranota/metaterga; the other, *xerophylla,* exhibits the typical red/blue pattern.

Components. — leucostriata Shelley, *xerophylla* Shelley.

The *Bidens* Group

Previously, the *bidens* group was monobasic, but I now add an undescribed species with a contiguous range to the north. It has been known for years, but thinking that it might be referrable to *Hubroria,* I withheld description until the validity of this name could be assessed. Whereas *bidens* has a long, narrow medial flange on the proximal part of the peak and a separate subconical tooth distal to the flange (Shelley 1981a), the new species lacks a tooth and its short medial flange has a broad variable lobe, arises distally on the peak, and terminates on the proximal part of the distal zone. Its affinity for *bidens* is demonstrated by the prefemoral processes. That of *bidens* is basally globose, while that of the new species is variable and moderately globose in the most proximal population. The *bidens* group occurs in the Sevier County, Tennessee, portion of the GSMNP, from Elkmont to Greenbrier.

Components. — bidens (Causey), *prolata,* new species.

Sigmoria (Falloria) prolata Shelley, new species   Figs. 77-83

Type specimens. — Male holotype (NCSM A1939) and 4 male and 7 female paratypes collected by R.M. Shelley and W.B. Jones, 19 May 1978, in the Ramsey Cascade Parking Area, Greenbrier Section, GSMNP, Sevier Co., TN. Male and female paratypes deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* with red paranota and blue transverse metatergal stripes; gonopods with following diagnostic characters: prefemoral process long, configuration variable, widest basally, tapering distad, extending beyond level of tip of acropodite; latter moderately thick and heavy, arch broadly curved and overhanging prefemoral process; basal zone continuous with peak and distal zone through broad, poorly defined anterior bend and apical curve; distal zone variable but generally moderately long, directed laterad from peak, not coplanar with basal zone, bent abruptly inward into arch at midlength in medial view; tip elongate and acuminate or reflexed; medial and lateral

flanges short, opposing each other on distal zone and distal extremity of peak, with variable lobes.

Color in Life. — Paranota red; metaterga black with wide, blue stripes along caudal edges connecting paranotal markings; collum with blue stripes along both anterior and posterior edges.

Holotype. — Length 41.1 mm, maximum width 9.7 mm, W/L ratio 23.6%, depth/width ratio 58.8%. Segmental widths as follows:

collum 7.8 mm	14th 9.4
2nd 8.6	15th 9.0
3rd 9.1	16th 8.5
4th 9.4	17th 7.3
5th-13th 9.7	18th 5.7

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 1.7 mm. Antennae extending back to caudal edges of 3rd paranota, relative lengths of antennomeres 2>3>6>5>4>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 10-10, labral 16-16.

Dorsum smooth, polished, with only faint wrinkling on anterior half of paranota. Collum broad, ends produced slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on 7-13, becoming progressively more acute posteriorly. Peritremata distinct, strongly elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum small, apically divided, much shorter than widths of adjacent coxae (Fig. 77); knobs between anterior legs of 5th sternum minute, lower than broad elevated areas between posterior legs; 6th sternum convexly recessed between 7th legs to accommodate apical curvature regions of acropodites. Postgonopodal sterna flat and plate-like, with bicruciform impressions on segments 8-9 and variably broad, shallow, central impressions on remaining segments. Coxae with low, blunt tubercles beginning on segment 8, becoming sharply acute on 10-15 and lowly rounded on remaining segments; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.0 mm, wide and 1.9 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface and thickened. Gonopods *in situ* (Fig. 78, of paratype) with acropodites overlapping near midlengths in midline of aperture, extending forward beyond anterior margin with distal zones crossing. Gonopod structure as follows (Figs. 79-80): Prefemoral process long, extending beyond level of tip of acropodite, widest basally, tapering smoothly and continuously to acuminate tip, latter curved gently anteriad, directed toward apical curve. Acropodite moderately thick, a broad, continuous curve with indistinguishable regions overhanging and extending well beyond level of prefemoral process; peak and basal zone continuous through anterior bend and continuous with distal zone through apical curve; distal zone moderately long, curving laterad and not coplanar with basal

Figs. 77-83. *Sigmoria (Falloria) prolata.* 77, process of 4th sternum of holotype, caudal view. 78, gonopods *in situ,* ventral view of paratype. 79, telopodite of left gonopod of holotype, medial view. 80, the same, lateral view. 81, telopodite of left gonopod of male from Porter Creek parking area, medial view. 82, distal part of acropodite of the same, lateral view. 83, telopodite of left gonopod of male from Roaring Fork Nature Trail, medial view. Scale line for fig. 78 = 1.00 mm; line for other figs. = 1.00 mm for 79-83, 1.33 mm for 77.

77

78

79

80

82

81

83
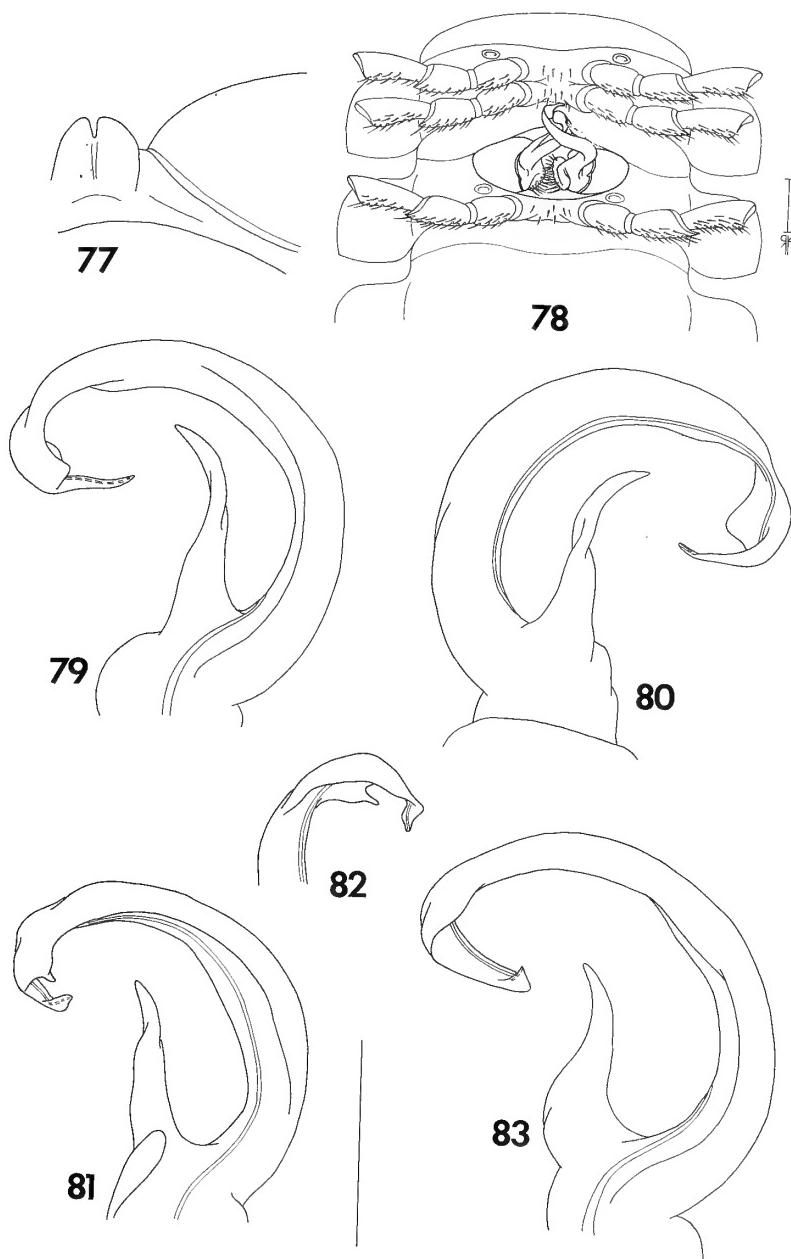
zone, bent abruptly inward into arch at midlength and tapering smoothly and continuously to acuminate tip; latter directed toward distal curve of prefemoral process; medial flange located opposite lateral flange, arising on distal extremity of peak, terminating in broad, triangular lobe at midlength of distal zone. Lateral flange arising at apical curve, terminating at midlength of distal zone, margin gently rounded. Prostatic groove crossing to lateral side on basal zone, continuing to terminal opening.

   Male Paratypes. — The male paratypes agree with the holotype in all particulars.

   Female Paratype. — Length 42.8 mm, maximum width 10.4 mm, W/L ratio 24.3%, depth/ width ratio 68.3%. Cyphopods *in situ* with corner of receptacles visible in apertures, valves directed caudolaterad. Receptable very large, completely enveloping valves, with ridges and lobes, surface rugulose. Valves small, subequal, surfaces finely granulate.

   Variation. — Considerable variation is evident in both the prefemoral process and acropodite of *prolata*. All samples from the Greenbrier section of the GSMNP differ from the types, which are from the northernmost point reachable by road in this area. Those from Porter Creek parking area (NCSM A3007), the southernmost point in Greenbrier, have a more linear prefemoral process, a shorter distal zone with a reflexed tip, and a short distal projection on the medial flange (Figs. 81-82). Males collected along Rhododendron Creek on the entrance road to Greenbrier (NCSM A1942) resemble those from Porter Creek except the medial flange is trapezoidal and lacks the projection. The male collected along Roaring Fork Nature Trail (NCSM A1895), about 4 miles south of Greenbrier, displays a broadly linear medial flange that is not rounded, a narrow and inconspicuous lateral flange, a long distal zone, a reflexed tip, and a prefemoral process that is moderately globose basally and similar to that in contiguous populations of *bidens* (Fig. 83). Thus specimens from the geographic extremes, Ramsey Cascade and Roaring Fork, exhibit long distal zones, but only those from the former have reflexed tips. There are also north-south geographic trends toward a narrower medial flange and a basally broader prefemoral process, which grades into the globose condition found in *bidens* (see Shelley 1981a, Figs. 80-81, p. 82).

   Ecology. — *Sigmoria (F.) prolata* is a cove inhabiting species.

   Distribution. — Known only from the Greenbrier and Roaring Fork sections of the GSMNP near Gatlinburg in Sevier County, Tennessee. I have searched in vain for *prolata* along TN highway 73, which runs along the western edge of the Park in Tennessee and connects these two sections, and thus believe it to be restricted to these secluded areas of the Park. The species is abundant in Greenbrier and can be easily collected in May or June. It is comparatively rare in Roaring Fork, however, as two subsequent trips to the site of the first collection failed to produce more individuals. Specimens were examined as follows:

   TENNESSEE: *Sevier Co.,* Greenbrier Section, GSMNP, 8.2 mi. ENE Gatlinburg, Ramsey Cascade pkg. area, 5M, 7F, 19 May 1978 (NCSM A1939) TYPE LOCALITY; 7.5 mi. ENE

Gatlinburg, Porter Creek pkg. area, 9M, 5F, 8 May 1980 (NCSM A3007); 4.0 mi. ENE Gatlinburg, along Greenbrier entrance rd. 1.8 mi. E jct. TN hwy. 73, 2M, 3F, 19 May 1978 (NCSM A1942); and unknown sites in Greenbrier, M, 14 June 1939, D.H. Lowrie, and M, 15 June 1942, C.H. Seevers (both RLH). Roaring Fork Nature Trail between 3rd and 4th bridges, 2.9 mi. ESE Gatlinburg, M, F, 16 May 1978 (NCSM A1895).

Remarks. — *Sigmoria (F.) prolata* links forms in the GSMNP, which are clearly referrable to *Sigmoria s. lat.,* with those in the Cumberland Plateau with laterally directed distal zones that could be assigned to *Hubroria.* Hence, this species is a major reason why the latter name is placed in synonymy.

The *Tuberosa* Group

The single species of this group is characterized by a number of apomorphic traits including hirsute postgonopodal sterna, a circular gonopodal aperture, tubercles on the outer surface of the basal zone of the acropodite, fusion of the tooth and medial flange, an additional flange on the inner surface of the distal zone, and a unique, complex tip. The species is known only from the eastern part of the GSMNP and adjacent areas in Swain County, North Carolina.

Component. — *tuberosa* Shelley.

The *Aphelorioides* Group

A single species group is proposed for *aphelorioides.* The general configuration of the prefemoral process is shared with *xerophylla* and *nantahalae,* and the circular acropodite is similar to that of *ainsliei;* however, there are important differences in the two loops as discussed in the species accounts. The *aphelorioides* group occurs between *xerophylla* and the *translineata* group in the Great Smoky Mountains south of the National Park. As with the latter, it spans the state line, occurring in the western fringe of North Carolina.

Components. — *aphelorioides,* new species.

Sigmoria (Falloria) aphelorioides Shelley, new species   Figs. 84-87

Type specimens. — Male holotype (NCSM A2468) and 3 male and 2 female paratypes collected by R.M. Shelley and W.B. Jones, 12 October 1978, from Monroe Co., TN, 17.3 mi. SE Madisonville, along TN highway 165, 0.5 mi W Bald River Falls, Cherokee National Forest. Three male

paratypes (A2466) taken by same collectors on same date, 14.3 mi SE Madisonville, along TN highway 165 at Tellico Ranger Station, Cherokee National Forest. Two male and one female paratypes (RLH) collected by L. Hubricht, 12 June 1953, from Monroe Co., 1.5 mi. E Tellico Plains, Tellico River Gorge. Male and female paratypes deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* without medial acropodal flange, with red paranota and blue transverse metatergal stripes, gonopods
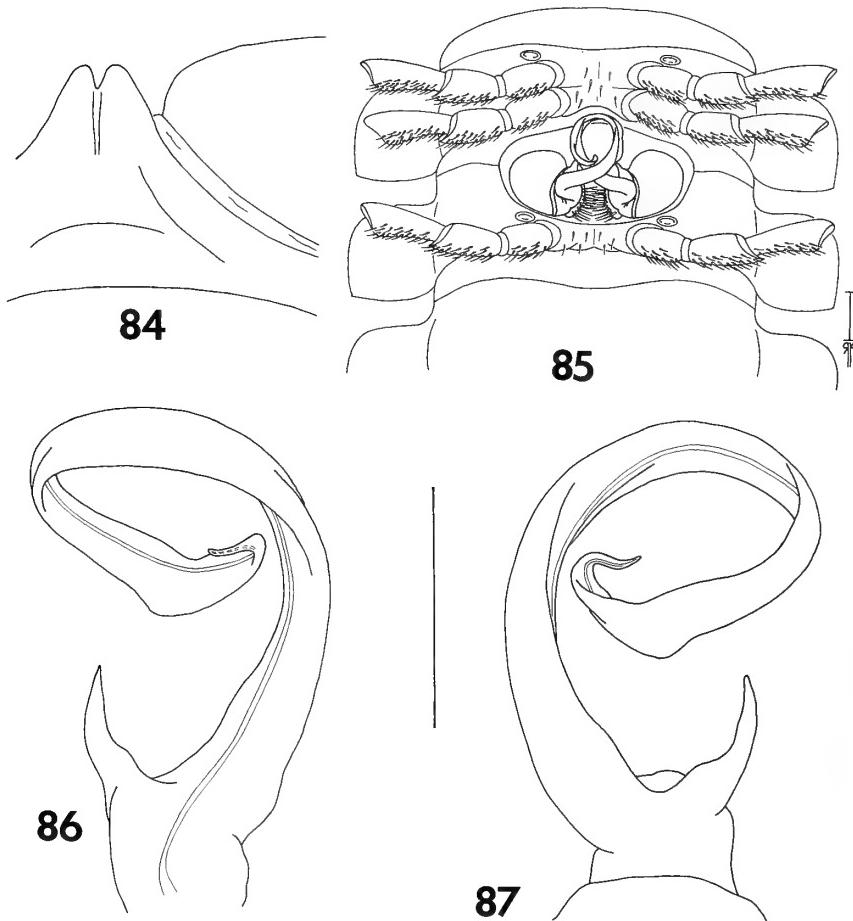
FIGS. 84-87. *Sigmoria (Falloria) aphelorioides.* 84, process of 4th sternum of holotype, caudal view. 85, gonopods *in situ,* ventral view of paratype. 86, telopodite of left gonopod of holotype, medial view. 87, the same, lateral view. Scale line for fig. 85 = 1.00 mm; line for other figs. = 1.00 mm for 84; 1.14 mm for 86-87.

with following diagnostic characters: acropodites *in situ* usually lying over and under one another; prefemoral process relatively long, upright, acuminate; acropodite moderately thick and heavy, slightly overhanging prefemoral process, configuration circular, anterior bend and apical curve broad but well defined, distal zone not coplanar with basal zone, extending laterad from peak, curving down behind arch of acropodite and extending nearly to level of basal zone, expanded proximal to tip, latter acuminate, bent abruptly dorsad.

Color in Life. — Paranota red; metaterga black with wide, blue transverse stripes along caudal edges connecting paranotal spots; collum with blue stripes along both anterior and caudal edges.

Holotype. — Length 42.4 mm, maximum width 10.7 mm, W/L ratio 25.2%, depth/width ratio 61.7%. Segmental widths as follows:

collum 7.0 mm	14th 10.5
2nd 8.9	15th 10.2
3rd 9.6	16th 9.9
4th-8th 10.4	17th 8.7
9th-13th 10.7	18th 6.1

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.8 mm, interantennal isthmus 1.9 mm. Antennae reaching back to middle of 4th paranota, relative lengths of antennomeres $2 > 3 > 4 = 5 = 6 > 1 > 7$. Genae with slight central impressions. Facial setae as follows: epicranial 1-1, interantennal and frontal absent, genal 2-2, clypeal about 15-15, labral about 18-18, merging with clypeal series and continuing for short distance along genal border, 2 setae per side.

Terga relatively coriaceous in middorsum, more so on paranota. Collum broad, ends extending well beyond those of following tergite. Paranota moderately depressed, angled ventrad and continuing slope of dorsum; caudolateral corners rounded on segments 1-4, becoming blunt and progressively more acute thereafter. Peritremata distinct, sharply elevated above metazonal surface; ozopores located in swelling just caudal to midlength, directed dorsolaterad.

Process of 4th sternum (Fig. 84) deeply divided apically, length subequal to widths of adjacent coxae; 5th sternum with small paramedial knobs between 4th legs and larger knobs between 5th legs; both shorter than widths of adjacent coxae; 6th sternum convexly recessed between 7th legs to accommodate curvature of acropodites. Postgonopodal sterna relatively flat and plate-like, with shallow central impressions, becoming deeper caudally. Coxal tubercles beginning on 10th legs, becoming longer and sharper posteriorly; prefemoral spines arising on segment 5, becoming progressively more acute caudally.

Gonopodal aperture broadly ovoid, 4.4 mm long and 1.9 mm wide at midpoint, indented anteriolaterad, sides strongly elevated above metazonal surface. Gonopods *in situ* (Fig. 95, of paratype) with acropodites lying over and under each other in midline of aperture, not intertwining, peaks extending forward just beyond anterior margin of aperture. Gonopod structure as follows (Figs. 86-87): Prefemur moderate in size, with relatively long, upright, acuminate prefemoral process arising on anterior side, bent slightly at midlength, with suggestion of tooth basally. Acropodite relatively thick and heavy, well sclerotized, circumscribing nearly complete circle of considerably more than one vertical plane, extending slightly beyond outer level of prefemoral process. Basal zone long, without modifications; anterior bend broad, well defined; peak gently curved and rounded, highest at midlength, leaning slightly mediad and

essentially coplanar with basal zone; apical curve relatively broad; distal zone long, extending laterad from peak and not coplanar with basal zone, expanding markedly near midlength then narrowing rapidly to acuminate tip; recurved and slightly bisinuate. Prostatic groove crossing to lateral side at anterior bend, running along inner surface of distal zone to opening at tip.

Male paratypes. — The prefemoral process is uncinate on a few paratypes, and the expansion of the distal zone is much broader in the males from Tellico Gorge.

Female paratype. — Length 42.7 mm, maximum width 10.7 mm, W/L ratio 25.1%, depth/width ratio 81.3%. Cyphopods *in situ* with side of receptacle visible in aperture, valves directed dorsad. Receptacle large, cupped over ventral surfaces of valves, surface rugulose. Valves relatively small, subequal, surfaces finely granulate.

Variation. — Neither size nor color pattern varies appreciably in *aphelorioides.* The most notable gonopodal variation involves the midlength expansion on the distal zone, which is broadest in the center of the range (Monroe Co.) and reduced in the eastern and western peripheries. The expansion is barely detectable in the male from North Carolina and resembles the condition in *ainsliei.* In the paratypes from Tellico Gorge and the male from McMinn County, the tip is broader and not as recurved as in other specimens (reflexed in the latter), and the distal part of the distal zone is "scoop-shaped."

Ecology. — *Sigmoria (F.) aphelorioides* inhabits moist rhododendron coves.

Distribution. — A small area in the Blue Ridge Province south of the Little Tennessee and north of the Hiwassee Rivers, lying just north of the area of *xerophylla.* In Tennessee the species in known only from the Cherokee National Forest, and it occurs in the Tellico Wildlife Management area in eastern Monroe County. The range extends across the North Carolina state line into the western fringe of Swain County, and *aphelorioides* should be expected in the Joyce Kilmer-Slickrock Wilderness Area of Graham County. Specimens were examined as follows:

TENNESSEE. *Monroe Co.,* 8.8 mi E Madisonville, along unnumbered rd. off co. rd. 2568, M, 3F, 13 October 1978 (NCSM A2475); 14.3 mi SSE Madisonville, along TN hwy. 165 at Tellico Ranger Station, 3M, 12 October 1978 (NCSM A2466); 17.3 mi SSE Madisonville, along TN hwy. 16, 0.5 mi W Bald River Falls, 4M, 2F, 12 October 1978 (NCSM A2468) TYPE LOCALITY; and 1.5 mi. E Tellico Plains, Tellico Gorge, 2M, F, 12 June 1953. L. Hubricht (RLH). *McMinn Co.,* 11.2 mi. SE Athens, along co. rd. 4371, 0.5 km W jct co. rd. 4276, M, F, 13 October 1978 (NCSM A2479).

NORTH CAROLINA: *Swain Co.,* 0.3 mi N Tapoco (in Graham Co.), along trail off US hwy. 129 just inside Graham Co. line, M, 26 June 1974 (NCSM 2460).

Remarks. — Though phenotypically similar to *ainsliei* in having a circular acropodite, *aphelorioides* differs in that the loop passes through considerably more than one vertical plane. In *aphelorioides* the distal zone curves laterad from the peak, whereas it is not coplanar with the basal zone in *ainsliei.* These looped or circular configurations are convergent with the

condition in *Apheloria,* hence *aphelorioides'* specific name; they are also convergent with that in *trimaculata (Rudiloria).* The distal zone is not broader at midlength in *ainsliei,* but most males of *aphelorioides* display a distinct expansion, particularly those from the center of the distribution. This expansion is in about the same position on the distal zone as the lobes in *trimaculata kleinpeteri (Rudiloria).* Thus, in the Great Smoky Mountains and from Virginia to Canada there are forms with circular acropodites that possess and lack an expansion on the distal zone. Their relative statuses, however, differ; those in the Smokies are reproductively isolated, whereas the others connect through intergrades and represent geographic races. In addition to the acropodal differences, the distinct prefemoral processes of *ainsliei* and *aphelorioides* also indicate reproductive isolation. In contrast, the projections of *t. trimaculata* and *t. kleinpeteri (Rudiloria)* are nearly identical.

The *Translineata* Group

Four species, two newly described, are added to the *translineata* group, bringing its composition to seven species, four in the Great Smoky Mountains area of Tennessee and North Carolina and three in the Cumberland Plateau of Tennessee. One species, *ainsliei,* occurs in the former and extends west into the fringe of the adjacent Ridge and Valley Province. The species are united by a divided prefemoral process; *translineata, lyrea, ainsliei,* and *forficata* have large, deeply divided structures, but it is shorter, and the division more shallow, in *fumimontis.* The processes are large and cupped, and the division subapical in *houstoni* and *abbreviata.* In *translineata, lyrea,* and *fumimontis* the peak is tilted laterad, and the medial flanges are long and narrow, arising on the anterior bend and terminating near the beginning of the apical curve. The first two also display a rounded lobe on the lateral edge of the acropodite near the beginning of the apical curve. The acropodal configurations vary, with *translineata* and *fumimontis* having flattened peaks and short distal zones, while *ainsliei* has a circular acropodite that forms a complete loop. *Sigmoria (F.) lyrea* exhibits an intermediate configuration but does not occupy an intermediate geographical position. In the Blue Ridge forms the distal and basal zones are coplanar, but the former curves strongly laterad in the Cumberland species and is nearly coplanar with the peak in *houstoni.* At first glance, *ainsliei* does not appear congeneric, as its circular acropodite is convergent with those in *Apheloria* (it was originally assigned to this genus by Chamberlin (1921)), and it also lacks acropodal adornments, most notably a medial flange.

Despite these differences, the divided prefemoral process of *ainsliei* is clearly indicative of shared ancestry with other members of the *translineata* group.

Components. — *translineata* Shelley; *lyrea* Shelley; *fumimontis* Shelley; *ainsliei* (Chamberlin); *forficata,* new species; *houstoni* Chamberlin; *abbreviata,* new species.
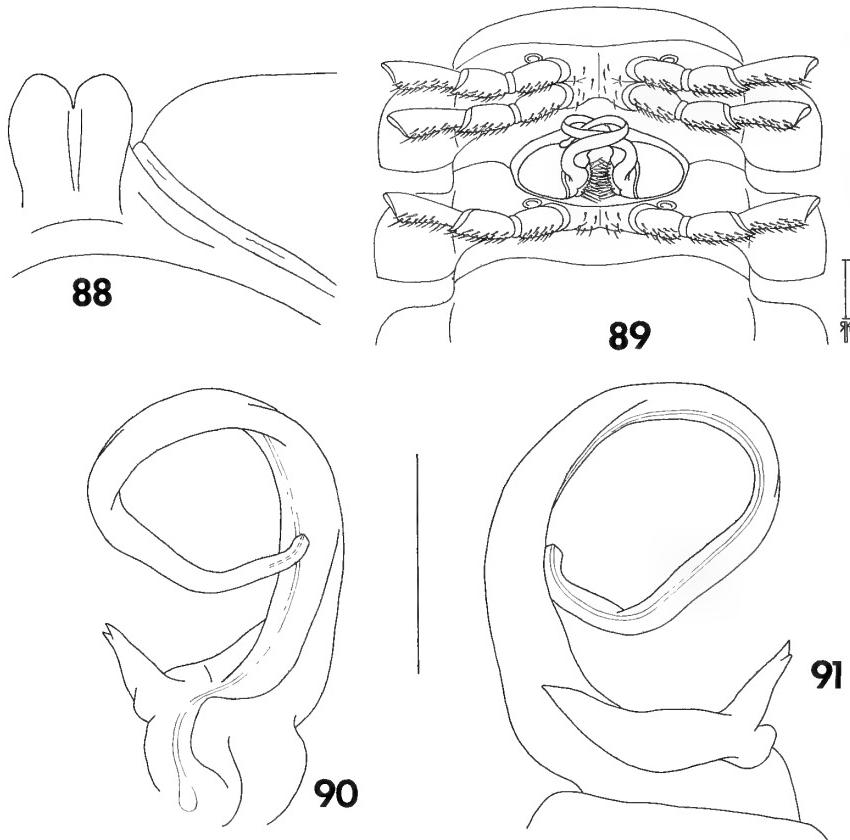
FIGS. 88-91. *Sigmoria (Falloria) ainsliei.* 88, process of 4th sternum of holotype, caudal view. 89, gonopods *in situ,* ventral view of male from Sevier Co., TN. 90, telopodite of left gonopod of holotype, medial view. 91, the same, lateral view. Scale line for fig. 89 = 1.00 mm; line for other figs. = 1.00 mm for 88 and 91; 1.33 mm for 90.

Sigmoria (Falloria) ainsliei (Chamberlin), new combination   Figs. 88-91

Apheloria ainsliei Chamberlin, 1921:232, Fig. 1. Attems, 1938:168, Fig. 184. Chamberlin and
    Hoffman, 1958:18.

Type specimen. — Male holotype (MCZ) collected by George G. Ainslie
on unknown date from unspecified locality in Knox Co., TN.

Diagnosis. — A large species of *Sigmoria* without medial acropodal
flange, usually with red paranota and blue transverse stripes along caudal
margins of metaterga; gonopods with following diagnostic characters:
acropodites interlocking and intertwined; prefemoral process large, divided
basally into two unequal components, lateral component longer and
directed laterad behind base of acropodite, medial component upright and
directed ventrad; acropodite moderately thick and heavy, slightly overhang-
ing prefemoral process, configuration circular, anterior bend and apical
curve broad but well defined, distal zone coplanar with basal zone, extend-
ing into arch and overlapping latter; tip narrowing on both sides to blunt,
central termination.

Color in Life. — Paranota usually red, occasionally blue, metaterga with blue stripes along
caudal margins.

Holotype. — Length 52.0 mm, maximum width 12.5 mm, W/L ratio 24.0%, depth/width
ratio 68.0%. Segmental widths as follows:

collum	9.0 mm	13th	12.3
2nd	10.4	14th	12.0
3rd	10.9	15th	11.5
4th	11.6	16th	10.6
5th-7th	12.0	17th	9.3
8th-12th	12.5	18th	6.4

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 2.0 mm. Antennae reaching back
to middle of 3rd paranota, relative lengths of antennomeres 2>3>4=5>6>1>7. Genae with
slight central impressions. Facial setae as follows: epicranial, interantennal, and genal absent,
clypeal about 12-12, labral about 16-16.

Terga smooth, polished, moderately coriaceous on paranota. Collum broad, ends extending
slightly beyond those of following tergite. Paranota moderately depressed, angled ventrad and
continuing slope of dorsum, caudolateral corners rounded through segment 5, blunt on 6-13,
becoming progressively more acute posteriorly. Peritremata relatively flat, not sharply elevated
above paranotal surface. Ozopores located in swellings near middle of paranota, opening dor-
solaterad.

Process of 4th sternum (Fig. 88) moderate, subequal to widths of adjacent coxae; 5th ster-
num with large paramedial knobs between both leg pairs, shorter than widths of adjacent cox-
ae; 6th sternum convexly recessed between both leg pairs to accommodate apical curvatures of
acropodites. Postgonopodal sterna relatively flat and plate-like, with large, shallow central im-
pressions on caudal segments and transverse grooves between leg pairs on all segments. Small
coxal tubercles present on legs of segments 9-16; prefemoral spines beginning on legs of seg-
ment 6, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 5.4 mm wide and 2.4 mm long at midpoint, indented anteriolaterad, sides raised above metazonal surface. Gonopods *in situ* (Fig. 89, not this specimen) with acropodites projecting ventrad from aperture, bending sharply mediad and overlapping and intertwining in midline, peaks extending forward beyond anterior edge of aperture and inserting in depression between 7th legs, apices directed ventrad on respective sides of aperture. Gonopod structure as follows (Figs. 90-91): Prefemur large, subglobose, with basally divided prefemoral process arising on anterior side, components of process diverging by more than 90°; lateral component longer than medial, directed laterad and extending behind base of acropodite, tip blunt, obscured in medial view; medial component apically bifurcate and upright, directed ventrad. Acropodite moderately thick and heavy, circumscribing complete circle of slightly more than one vertical plane, extending only to outer level of prefemoral process. Basal zone long, without modifications; anterior bend broad, well defined; peak gently curved and rounded, highest at midlength, leaning mediad and overhanging prefemur, not coplanar with basal zone; apical curve relatively broad but well defined; distal zone long, curving broadly into arch and overlapping basal zone, thus forming complete circle with peak and distal extremity of basal zone, essentially coplanar with peak, bent slightly at midlength and again just proximal to tip; latter blunt, directed subventrad, only slightly discontinuous with distal zone. Medial and lateral flanges absent. Prostatic groove crossing to lateral side of acropodite at anterior bend and continuing to opening in center of tip.

Description of Female. — Based on specimen from 16.3 km E Maryville, Blount County, TN (NCSM A2460).

Length 55.5 mm, maximum width 12.4 mm, W/L ratio 22.3%, depth/width ratio 78.2%. Cyphopods *in situ* with edge of receptacle visible in aperture, valves directed dorsolaterad. Receptacle large, globose, located entirely on medial sides of valves, surfaces rugulose. Valves moderate and subequal in size, diverging dorsad, surfaces finely granulate.

Variation. — *Sigmoria (F.) ainsliei* varies considerably in size, with some individuals dramatically larger than others. Dimensions of the male and a female from 10.2 miles east of Maryville (NCSM A2460) were 56.1 mm in length and 12.8 mm in width, and 59.8 mm in length and 13.3 mm in width, respectively. On the gonopods the prefemoral process is highly variable. Males from Knox County possess a simple, two-pronged structure, as described for the holotype, but most individuals from Blount and Sevier counties have one or two additional spurs on the ventral surface arising near the juncture of the two components. The configuration of the acropodite is reasonably constant, but the distal zone is slightly bisinuate in a few males and widens distally (proximal to the bend at the tip) in ones from the southern part of the range.

Ecology. — In the Blue Ridge Province in and near the GSMNP, *ainsliei* inhabits the moist rhododendron coves typical of *Sigmoria s. lat.* However, these environments are rare in the more western Ridge and Valley Province, particularly in the valley between the Smokies and Knoxville. Here I have found *ainsliei* in several predominantly hardwood habitats under leaves near water, but sample A2460 was taken under thick layers of leaves on a steep bank.

Distribution. — A small area in the adjacent fringes of the Ridge and Valley and Blue Ridge Provinces, ranging from just north of the French Broad River on the University of Tennessee campus in Knoxville to Tennessee Highway 73 (Little River Road) in the GSMNP. The species does not penetrate far into the GSMNP and has not been encountered east of Highway 73, for example along the road to Cades Cove. However, *ainsliei* is common in the Park near the Sinks, Metcalf Bottoms Picnic Area, and Little Greenbrier School, as well as in adjacent areas outside the park near Townsend and Wear Valley. It should be expected in western Sevier County and in the corner of Loudon County near Friendsville, although these areas contain so much cleared land that suitable milliped habitat is rare. Specimens were examined as follows:

TENNESSEE: *Knox Co.,* locality and date unspecified, M, G.G. Ainslie (MCZ) TYPE SPECIMEN; Knoxville, Cherokee Bluff, 2M, 17 May 1951, L. Hubricht (RLH) and University of Tennessee campus, M, 18 April 1972, W. Tolbert (RLH). *Blount Co.,* 10.2 mi E Maryville, along unnumbered rd., 1.0 km N jct. co. rd. 2427, M, 2F, 11 October 1978 (NCSM A2460); 6.4 me SE Maryville, along unnumbered rd., 3.2 km N jct. Foothills Parkway, F, 11, October 1978 (NCSM A2462); 3.4 mi N Townsend along co. rd. 2422, M, 9 April 1981 (NCSM A3659); and GSMNP, along TN hwy. 73 at crossing of Little R., M, F, 17 May 1978 (NCSM A1932). *Sevier Co.,* 1.4 mi. W Gatlinburg, along Norton Creek Rd. off US Hwy. 441, 3M, F, 8 May 1980 (NCSM A3015); Little Greenbrier School, GSMNP, 5M, 6F, 17 May 1978 (NCSM A1935); and GSMNP, along TN hwy 73, 0.6 mi N Metcalf Bottoms Picnic Area, 2M, F, 9 August 1981, R.M. Shelley and H. Enghoff (NCSM A3723).

Remarks. — *Sigmoria (F.) ainsliei* lacks a medial flange, but a new medial edge arising at the anterior bend is suggestive of a flange. This is actually caused by torsion. The medial surface of the basal zone shifts to the lateral side at the anterior bend, and a new medial edge arises at this point, extends the length of the peak, and terminates at the apical curve, whereupon a third medial edge arises. The acropodite is not broader through the peak, at it would be with a flange, and tapers into the distal zone.

Sigmoria (Falloria) forficata Shelley, new species   Figs. 92-96

Type specimens. — Male holotype (NCSM A2630) and two male and two female paratypes collected by R.M. Shelley and R.K. Tardell, 7 May 1979, 4.2 mi. SE Crab Orchard, along Fall Creek near Ozone Twp., Cumberland Co., TN. Male and female paratypes deposited in FSCA.

Diagnosis. — A large species of *Sigmoria* with medial flange extending between proximal parts of peak and distal zone and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process massive, usually divided basally into two long com-

ponents, medial one shorter and usually more linear, lateral one longer and curved broadly anteriad; acropodite relatively thin, arch broadly curved
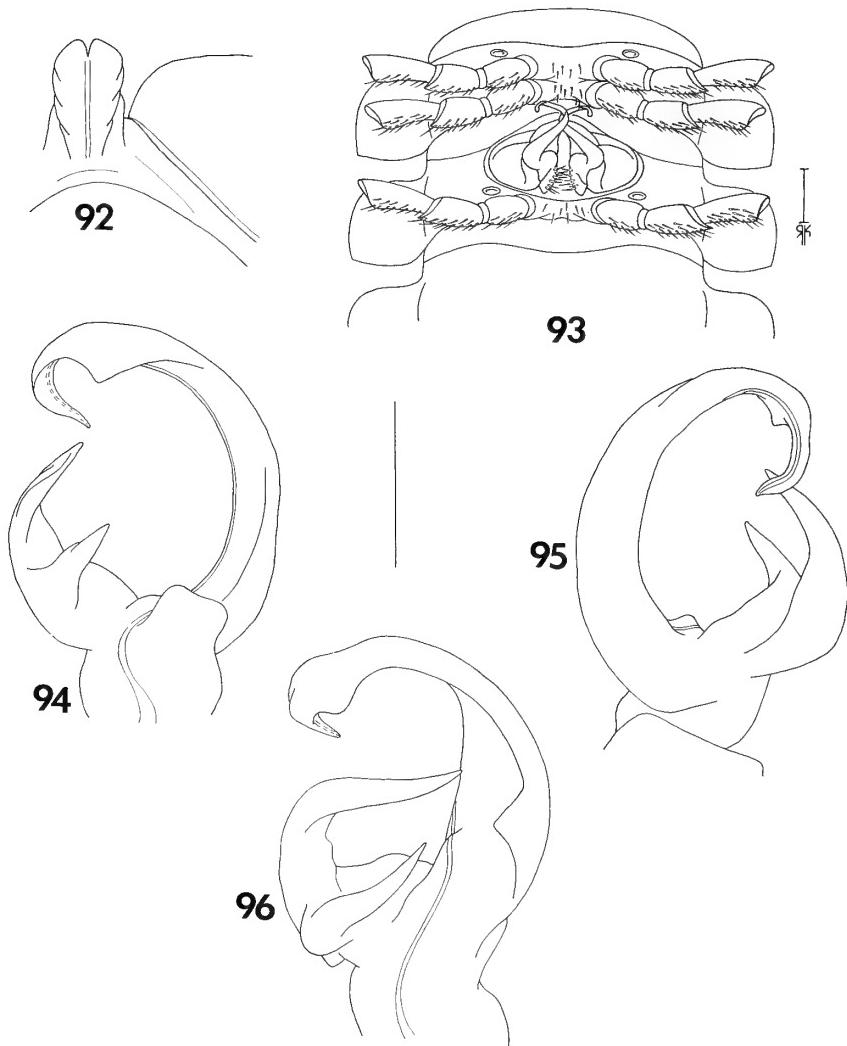
FIGS. 92-96. *Sigmoria (Falloria) forficata.* 92, process of 4th sternum of holotype, caudal view. 93, gonopods *in situ,* ventral view of paratype. 94, telopodite of left gonopod of holotype, medial view. 95, the same, lateral view. 96, telopodite of left gonopod of male from Scott Co., TN, medial view. Scale line for fig. 93 = 1.00 mm; line for other figs. = 1.00 mm for each.

and extending over prefemoral process; basal zone gently curved, with or without a basomedial projection; anterior bend and apical curve poorly defined; distal zone moderately long, directed laterad from peak and not coplanar with other sections, curving into arch distad and tapering to acuminate tip; medial flange variable but with broadly triangular lobe on distal extremity of peak; lateral flange inconspicuous, a small lobe on distal zone opposite distal extremity of medial flange.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal edges connecting paranotal markings; collum with blue stripes along both anterior and posterior margin.

Holotype. — Length 48.8 mm, maximum width 11.3 mm, W/L ratio 23.2%, depth/width ratio 58.4%. Segmental widths as follows:

collum 6.8 mm	14th 10.8
2nd 8.5	15th 9.8
3rd 9.9	16th 9.5
4th 10.3	17th 8.4
5th-6th 10.8	18th 6.3
7th-13th 11.3	

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.9 mm, interantennal isthmus 1.7 mm. Antennae relatively long, reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres $2>3>6>4=5>1>7$. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, frontal 1-1, genal 2-2, clypeal about 12-12, labral about 16-16.

Dorsum smooth, polished, and moderately coriaceous, especially on anterior halves of paranota. Collum broad, ends extending well below those of following tergite. Paranota strongly depressed, angling sharply downward and exceeding slope of dorsum, caudolateral corners rounded through segment 7, blunt on 8-13, and becoming progressively more acute posteriorly. Peritremata relatively flat and indistinguishable, ozopores located near middle of peritremata, opening dorsolaterad.

Sternum of segment 4 with long, apically divided process, longer than widths of adjacent coxae (Fig. 92); that of segment 5 with long apically divided process between anterior legs and two medially coalesced knobs between 5th legs, projections nearly equal in length to each other and to widths of adjacent coxae; 6th sternum deeply and convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna as follows: those of segments 8-10 with flattened elevated areas and blunt caudally directed lobes subtending anterior and posterior coxae, respectively, these strongest on segment 8 and progressively less pronounced on 9-10; remaining sterna without elevations between anterior legs and with progressively smaller ones between posterior legs, becoming progressively more plate-like posteriorly with variably broad central impressions. Coxae with blunt tubercles beginning on caudal legs of segment 9, sharply acute on 11-14, diminishing thereafter; prefemoral spines on segment 5, becoming progressively longer and more acute posteriorly.

Gonopodal aperture ovoid, 4.6 mm wide and 2.6 mm long at midpoint, strongly indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 93, of paratype) with acropodites angling mediad and overlapping in midline of aperture, then curving laterad and extending slightly beyond anterior margin; prefemoral processes with components crisscrossing. Gonopod structure as follows (Figs. 94-95): Prefemoral process massive, divided basally into two components, a short, straight medial one, and a longer, broadly curved

anterior one, both directed toward basal zone and tapering smoothly and continuously to acuminate tips. Acropodite rather thin, forming broadly curved arch, extending nearly to level of distal extremity of prefemoral process; basal zone gently curved, continuous with peak through anterior bend; latter broad, poorly defined; peak gently curved, apex near midlength; apical curve broad, poorly defined; distal zone moderately long, curving laterad from peak and not coplanar with basal zone or peak, curving inward distally and tapering to acuminate tip; latter directed toward basal zone. Medial flange large and conspicuous, broadly triangular, arising on proximal part of peak, terminating on proximal part of distal zone. Lateral flange small and inconspicuous, a broadly rounded lobe opposite distal half of medial flange. Prostatic groove crossing to lateral side on peak and continuing to terminal opening.

Male Paratypes. — The male paratypes agree with the holotype in all particulars.

Female Paratype. — Length 47.0 mm, maximum width 11.3 mm, W/L ratio 24.0%, depth/width ratio 69.9%. Cyphopods *in situ* with corners of receptacles partly visible in aperture, partially obscured by large, convoluted cyphopodal membranes, valves directed caudad. Receptable moderately large, completely enveloping valves, with lobes and ridges, surface rugulose. Valves small, subequal, surfaces finely granulate.

Variation. — The sternal projections are similar to those of the holotype in all males except those from Hamilton County, where they are smaller. In this individual the process on segment 4 is equal in length to the widths of the adjacent coxae; the anterior projection on segment 5 is absent; and there are broad, separate, elevated areas between the posterior legs that are much shorter than the adjacent coxal widths. The postgonopodal sternal lobes on segments 8-10 are also smaller.

On the gonopods, the males from Cumberland County agree closely with the holotype, although that from 8.5 miles E of Crab Orchard (NCSM A2766) has a small triangular projection from the medial edge of the basal zone near midlength. The male from Scott County, the northernmost locality, has a more rounded medial flange that arises proximally on the basal zone and has a distinct spine from the proximomedial edge (Fig. 96). The latter closely resembles the condition in *arcuata (Cleptoria)* in piedmont South Carolina. The Morgan County male has a broad prefemoral process that is cupped on the ventral surface and not as deeply divided, so the medial projection appears more as a basal spur than a separate structure. The medial flange in the Morgan County male is less expanded and terminates more abruptly on the distal zone. South of Cumberland County, the Bledsoe County male is nearly identical to the holotype, but in those from Hamilton County, the medial component of the prefemoral process is longer and curved toward the other, which in turn is narrower and more sinuous than in the holotype.

Ecology. — *Sigmoria (F.) forficata* is a cove inhabiting species.

Distribution. — The Cumberland Plateau of Tennessee. *Sigmoria (F.) forficata* occurs sporadically across the width of Tennessee from near the Kentucky to near the Georgia/Alabama borders. It may eventually be dis-

covered in McCreary County, Kentucky, but the Tennessee River marks its
southern range limit, as extensive searches south of the waterway in Marion
and Hamilton counties, and adjacent parts of Georgia and Alabama, have
been unsuccessful. Specimens were examined as follows:

TENNESSEE. — *Scott Co.,* 7.0 mi. S. Huntsville, along co. rd. 2342 near Brimstone Cr.,
M, F, 8 June 1979 (NCSM A2724). *Morgan Co.,* 4.3 mi. SW Wartburg, along Emory R. on
edge of Catoosa Wildlife Man. Area, M, 2F, 7 June 1979 (NCSM A2718). *Cumberland Co.,*
8.5 mi. N Crossville, along Fox Cr. in Catoosa Wildlife Man. Area, M, 2F, 15 June 1979
(NCSM A2765); 4.2 mi. SE Crab Orchard, along Falls Cr. near Ozone, 3M, 2F, 7 May 1979
(NCSM A2630) TYPE LOCALITY; and 8.5 mi. E Crab Orchard, along co. rd. 4382, 2.2 mi.
W jct. co. rd. 2590, M, 2F, 15 June 1979 (NCSM A2766). *Bledsoe Co.,* 2.8 mi. SE Pikeville,
along TN hwy. 30, M, F, 25 May 1983 (NCSM A4137). *Hamilton Co.,* Signal Mountain, M, F,
18 August 1956, R.L. Hoffman (RLH); and Rainbow Lake Wilderness Area nr. Signal Moun-
tain, M, 22 May 1983 (NCSM A4113).

Remarks. — Some traits of *forficata* are convergent with ones found in
congeners in piedmont South Carolina, many miles east across the Ap-
palachians. The large, convoluted cyphopodal membrane is similar to that
in *catawba, saluda,* and *simplex (Croatania);* and the long process on the
4th sternum closely resembles those in these species plus *shelfordi* and *ar-
cuata (Cleptoria).* The distinct basal spine on the medial flange in the Scott
County male also resembles those in these species as does the slightly distal
triangular lobe in a Cumberland County male. Lastly, the prefemoral proc-
ess is massive in *forficata, catawba,* and *saluda,* and the curvature of the
lateral component is similar to that of the entire structure in *catawba* and
saluda (compare Figs. 30 and 32 with Figs. 1, 3, 7, and 8 in Shelley 1977).

Sigmoria (Falloria) abbreviata Shelley, new species   Figs. 97-100

Type specimens. — Male holotype (A4136) and one male and three
female paratypes collected by R.M. Shelley, 24 May 1983, from Fall Creek
Falls State Park, Van Buren Co., TN. Additional paratypes collected in
same locality as follows: two females by same collector, 17 June 1976; and
one male and four females by R.M. Shelley and R.K. Tardell, 13 May 1979.
Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on
distal extremity of peak and with red paranota and blue metatergal stripes;
gonopods with following diagnostic characters: prefemoral process large,
ventral surface convex distad, divided at midlength into two subequal,
diverging components; acropodite thin and fragile, arc broadly curved and
extending over but not beyond level of prefemoral process; basal zone

broadly curved; anterior bend and apical curve poorly defined; peak and distal zone relatively short; latter curving sublaterad from former, not coplanar with other sections, bent into arch distad and tapering to acuminate tip; medial flange a small, rounded lobe; lateral flange narrow
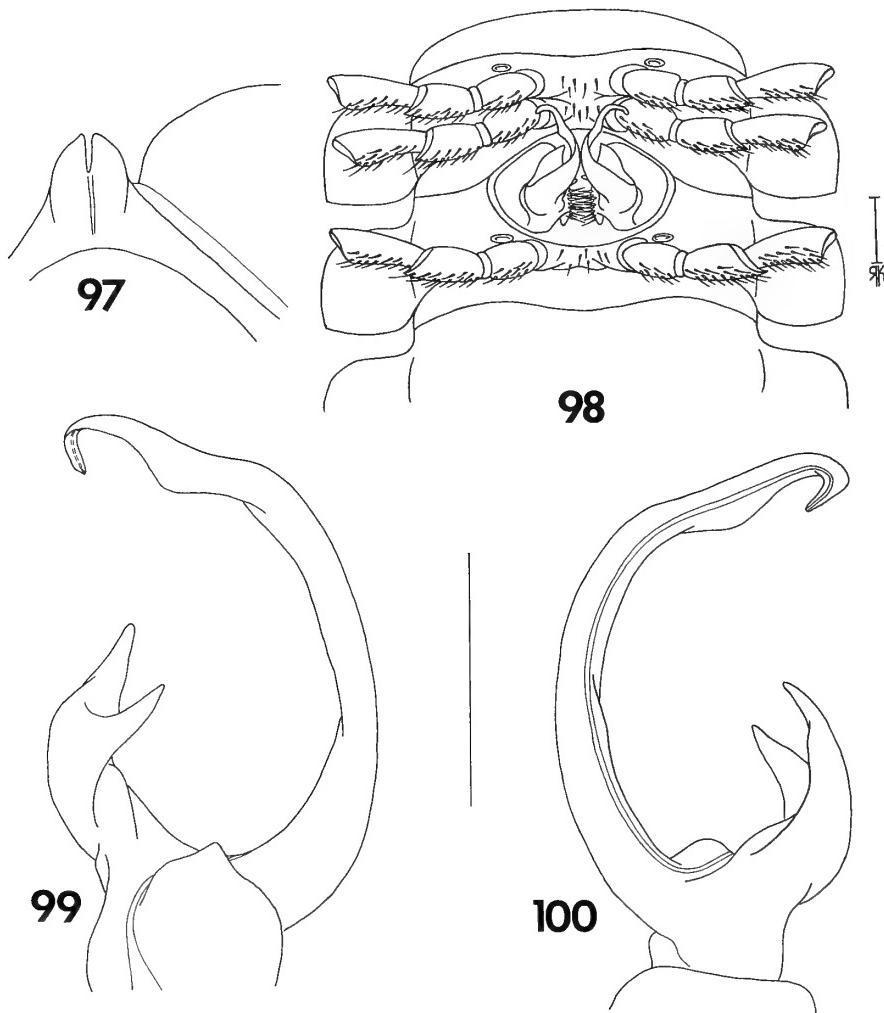
FIGS. 97-100. *Sigmoria (Falloria) abbreviata.* 97, process of 4th sternum of holotype, caudal view. 98, gonopods *in situ,* ventral view of paratype. 99, telopodite of left gonopod of holotype, medial view. 100, the same, lateral view. Scale line for fig. 98 = 1.00 mm; line for other figs. = 1.00 mm for 99-100; 1.33 mm for 97.

and inconspicuous, represented by a slightly wider acropodite stem opposite medial flange.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal margins connecting paranotal spots; collum with blue stripes along both anterior and posterior edges.

Holotype. — Length 37.0 mm, maximum width 9.1 mm, W/L ratio 24.6%, depth/width ratio 60.4%. Segmental widths as follows:

collum 6.9 mm	15th 8.9
2nd 7.2	16th 8.7
3rd 7.9	17th 7.5
4th 8.8	18th 5.4
5th-14th 9.1	

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.4 mm, interantennal isthmus 1.4 mm. Antennae reaching back to middle of 3rd paranota, relative lengths of antennomeres 2>3>5>6=4>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 16-16, labral 22-22.

Dorsum smooth, polished, moderately coriaceous. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on 7-13, becoming progressively more acute caudally. Peritremata thick and conspicuous, strongly elevated above paranotal surface, ozopores located caudal to midlength, opening dorsolaterad.

Process of 4th sternum moderately long, equal to widths of adjacent coxae (Fig. 97); 5th sternum with two paramedian knobs between anterior legs, shorter than widths of adjacent coxae, and broad, flattened, elevated areas between posterior legs; 6th sternum convexly recessed between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna with bicruciform impressions on 8-9, becoming progressively flatter and more plate-like posteriorly with variably broad, shallow, central impressions. Coxae with blunt tubercles beginning on segment 10, becoming progressively more acute posteriorly; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 3.4 mm wide and 1.7 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 98, of paratype) with acropodites angling toward midline, either touching or overlapping near midlengths, then curving anteriolaterad and extending beyond anterior margin. Gonopod structure as follows (Figs. 99-100): Prefemoral process large, curving slightly ventrad at midlength and convex distally on ventral surface, divided into two diverging, subequal, acuminate components, directed toward midlength of acropodite. Acropodite moderately thin, forming broadly curved arc, overhanging prefemoral process; basal zone broadly curved, continuous with peak through anterior bend; latter broad, poorly defined; peak moderately long; apical curve broad, poorly defined; distal zone relatively short, curving sublaterad from peak and not coplanar with other sections, bending inward into arch distad and tapering to blunt tip. Medial flange small, margin smoothly rounded, located on distal extremity of peak. Lateral flange barely detectable, a slightly wider spot in stem of acropodite opposite medial flange. Prostatic groove crossing to lateral side on basal zone, continuing to terminal opening.

Male Paratypes. — The only variation in the male paratypes involves the shape and relative lengths of the projections of the prefemoral process.

Female Paratype. — Length 39.6 mm, maximum width 9.9 mm, W/L ratio 25.0% depth/width ratio 59.6%. Cyphopods *in situ* with corners of receptacles protruding through

folded, convoluted membranes in aperture, valves directed caudomediad. Receptacle large, located along anterior sides of valves, with ridges and lobes, surface rugulose. Valves moderate, subequal, surfaces finely granulate.

Variation. — The Bledsoe County male agrees with the holotype.

Ecology. — *Sigmoria (F.) abbreviata* is a cove inhabiting species.

Distribution. — Known only from the central Cumberland Plateau. Specimens were examined as follows:

TENNESSEE. — Van Buren Co: Fall Creek Falls St. Pk., 2F, 17 June 1976 (NCSM A888), M, 4F, 13 May 1979 (NCSM A2693), and 2M, 3F, 24 May 1983 (NCSM A4136) TYPE LOCALITY. *Bledsoe Co.,* 22 mi. E Spencer, along TN hwy 30, 0.5 mi. E jct. TN hwy. 101, M, 2F, 14 May 1979 (NCSM A2697).

Remarks. — I have collected *abbreviata* two places in Fall Creek Falls State Park. The sample with the holotype came from behind the park office; the others were taken along the trails behind the nature center.

Although it has a bifurcate prefemoral process, *abbreviata* shares more features with *houstoni* than with *forficata*. The bifurcation is more of an elaboration on the squared/cupped condition found in *houstoni,* as the corners are elongated and the margin between them depressed, than it is true bifurcation, in which separate projections arise from a common base. The affinity between *abbreviata* and *houstoni* is also seen in the acropodites, as the medial flanges are in the same general locations, and the distal zones have the same general curvatures. The flange and distal zone are shorter (abbreviated) in *abbreviata,* hence the specific name. These is no indication of a flange on the basal zone in *abbreviata* as in some variants of *forficata,* and *abbreviata* also lacks the sternal modifications of the latter. Perhaps *abbreviata* and *houstoni* were once joined by intergrade forms that have disappeared leaving two isolated populations. Both warrant specific recognition because of these differences.

Sigmoria (Falloria) houstoni Chamberlin   Figs. 101-104

Sigmoria houstoni Chamberlin, 1943:144, Fig. 1. Hoffman, 1950:5. Chamberlin and Hoffman, 1958:50.

Type specimens. — Male holotype and female allotype (RVC); locality, date, and collector unknown. The vial label and the three prior references give Houston, Harris County, Texas, as the type locality, but this is clearly the result of a sampling mixup. As shown in Fig. 151, no member of the tribe Apheloriini occurs within 250 miles of Houston. The type locality should be somewhere in Franklin, Grundy, or Marion counties, Tennessee, the only places where *houstoni* has been authentically taken. The date of

collection and the collector reported by these authors may also be wrong. Because of this confusion, the following description is of a male collected from Marion County, along TN highway 108, 5.8 mi S of the Grundy County line.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange extending between midlengths of basal and distal zones and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process moderately long, ventral surface convex distad, apical margin with corners produced, with or without additional spurs; acropodite
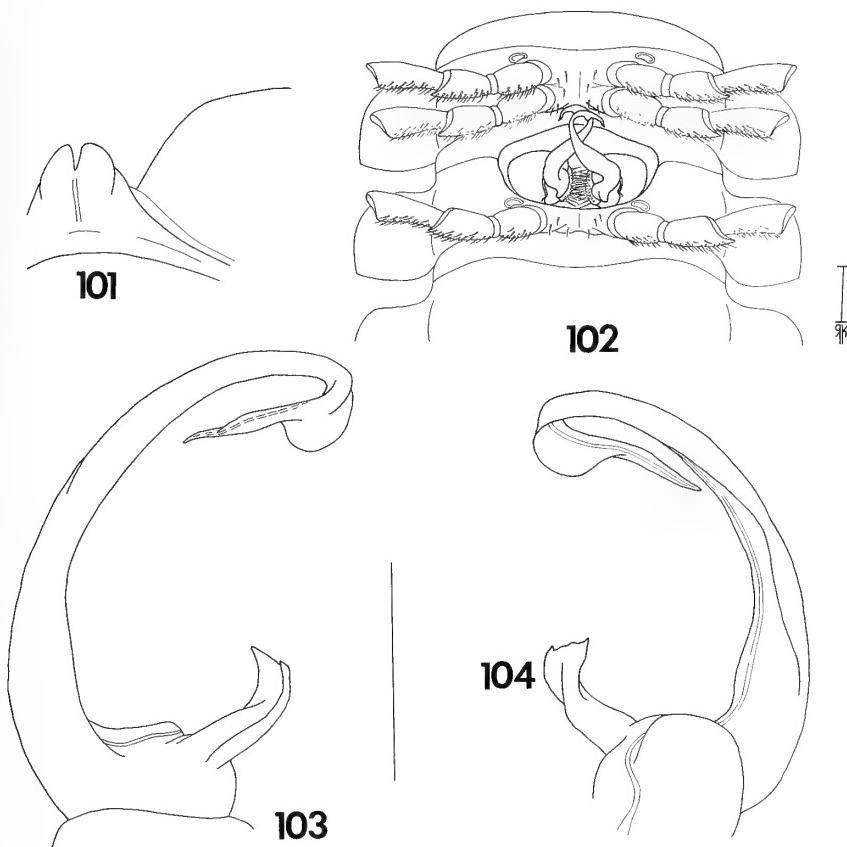
FIGS. 101-104. *Sigmoria (Falloria) houstoni.* 101, process of 4th sternum of male from Marion Co., TN, caudal view. 102, gonopods *in situ,* ventral view of the same. 103, telopodite of left gonopod of the same, submedial view. 104, the same, lateral view. Scale line for fig. 102 = 1.00 mm; line for other figs. = 1.00 for 101 and 104; 1.14 mm for 103.

relatively thin, curving broadly over but not beyond distal extremity of prefemoral process; basal zone gently curved; anterior bend poorly defined; peak short, continuing overall curvature of acropodite; apical curve well defined; distal zone relatively long, directed laterad and coplanar with peak, tapering distally to acuminate tip; medial flange long and narrow, expanded into rounded terminal lobe on proximal part of distal zone; lateral flange absent.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal edges connecting paranotal markings; collum with blue stripes along both margins.

Description. — Length 37.1 mm, maximum width 8.9 mm, W/L ratio 24.0%, depth/width ratio 48.3%. Segmental widths as follows:

collum	5.8 mm	14th	8.4
2nd	6.9	15th	8.1
3rd-4th	7.9	16th	7.5
5th-7th	8.7	17th	6.5
8th-13th	8.9	18th	5.0

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.1 mm, interantennal isthmus 1.3 mm. Antennae relatively short, extending only to caudal edge of 2nd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 10-10, labral 12-12.

Dorsum smooth, moderately coriaceous in midline. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 4, blunt in midbody region, becoming progressively more acute caudally. Peritremata distinct, strongly elevated above paranotal surface; ozopores located caudal to midlength, opening dorsolaterad.

Sternum of segment 4 with small lobe between 3rd legs, much shorter than widths of adjacent coxae (Fig. 101); that of segment 5 with low knobs between 4th legs, much shorter than widths of adjacent coxae, and low flattened areas between 5th legs; sternum of segment 6 convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna smooth and flat, bicruciately impressed on segments 8-10, with variably broad, shallow, central impressions on remaining segments. Coxae with blunt tubercles beginning on segment 5, sharp and distinct on all legs.

Gonopodal aperture elliptical, 2.9 mm wide and 1.6 mm long at midpoint, indented slightly anteriolaterad, sides raised above metazonal surface. Gonopods *in situ* (Fig. 102) with acropodites angling mediad and overlapping in midline of aperture, curving laterad, overlapping again, and projecting slightly beyond anterior margin. Gonopod structure as follows (Figs. 103-104): Prefemoral process moderately large, rectangular, narrowest basally, convex ventrally, distal corners curved ventrad and directed toward basal zone. Acropodite thin and laminate, forming broadly curved, open arc, extending over but not beyond level of distal extremity of prefemoral process; basal zone gently curved, continuous through anterior bend with peak; anterior bend broad, poorly defined; peak continuing general curvature of basal zone and anterior bend; apical curve short, well defined; distal zone moderately long, curving directly laterad and coplanar with peak, tapering smoothly and continuously to acuminate tip, latter slightly bisinuous. Medial flange long, arising proximally on basal zone, continuing through peak as linear lamina, expanding into rounded lobe on proximal part of distal zone, terminating abruptly at distal extremity of lobe near midlength of distal zone. Lateral flange

absent. Prostatic groove crossing from medial to lateral sides around proximal part of peak, continuing to terminal opening.

Description of Female from Grundy Co. — Length 42.8 mm, maximum width 10.6 mm, W/L ratio 24.8%, depth/width ratio 69.8%. Cyphopods *in situ* with corners of receptacles protruding through folded, convoluted membranes in aperture, valves directed caudomediad. Receptacle large, located along anterior sides of valves, with ridges and lobes, surface rugulose. Valves moderate, equal, surfaces finely granulate.

Variation. — The gonopods of *houstoni* are rather uniform. Some prefemoral processes are more elaborate than others and have short terminal and subterminal spurs, but this is random variation with no geographic component. Similarly, the medial flange widens slightly basally then narrows again at the approximate location of the anterior bend in some males.

Ecology. — The specimens of *houstoni* I collected came from dry, open, hardwood litter well removed from water. It therefore is not a cove species and has different ecological preferences from *forficata* and the Appalachian congeners.

Distribution. — Cumberland Plateau of Grundy, Marion, and Franklin counties, Tennessee. It should also be expected in the western fringe of Sequatchie County. Specimens were examined as follows:

TENNESSEE. — *Grundy Co.,* 4 mi. N Palmer, along co. rd. 4350, 23 May 1983 (NCSM A4122); 2.5 mi. S Palmer, along TN hwy. 108, 0.3 mi. N Marion co. line, M, 2F, 12 May 1979 (NCSM A2684); and Grundy St. For. near Tracy City, 2M, 2F, 26 April 1979 (A2606). *Marion Co.,* 11.1 mi. N Whitwell, along TN hwy. 108, 1.8 mi. S Grundy co. line, M, 26, April 1979, A.L. Braswell, R.E. Ashton, and R. Franz (NCSM A2589); 5.8 mi. S Grundy co. line, along TN hwy. 108, 3M, 3F, 12 May 1979 (NCSM A2685) and 3.5 mi. N Whitwell, along TN hwy. 108, 0.9 mi. S. jct. co. rd. 4303, 2M, 23 May 1983 (NCSM A4121). *Franklin Co.,* Sewanee, 2M, date unknown, S. Lazell (FSCA).

Remarks. — Because the distal zone curves directly laterad and thus is coplanar with the peak, the acropodite was tilted slightly ventrad in figure 103 to show this section.

The *Picapa* Group

A single species group is proposed for *picapa,* which differs from the other Cumberland species in the large, bisinuate, undivided prefemoral process. The laterally directed distal zone is not reflective of a separate genus as Keeton (1960) thought when he described it. The species is not a cove inhabitant and is known only from a small area in northern Morgan County, Tennessee.

Component. — *picapa* (Keeton).

Sigmoria (Falloria) picapa (Keeton), new combination   Figs. 105-108

Hubroria picapa Keeton, 1960:2-4, Figs. 1-4.

Type specimens. — One male and two female paratypes (FMNH) collected by B. Benesh, June 1949, at Sunbright, Morgan Co., TN. Male
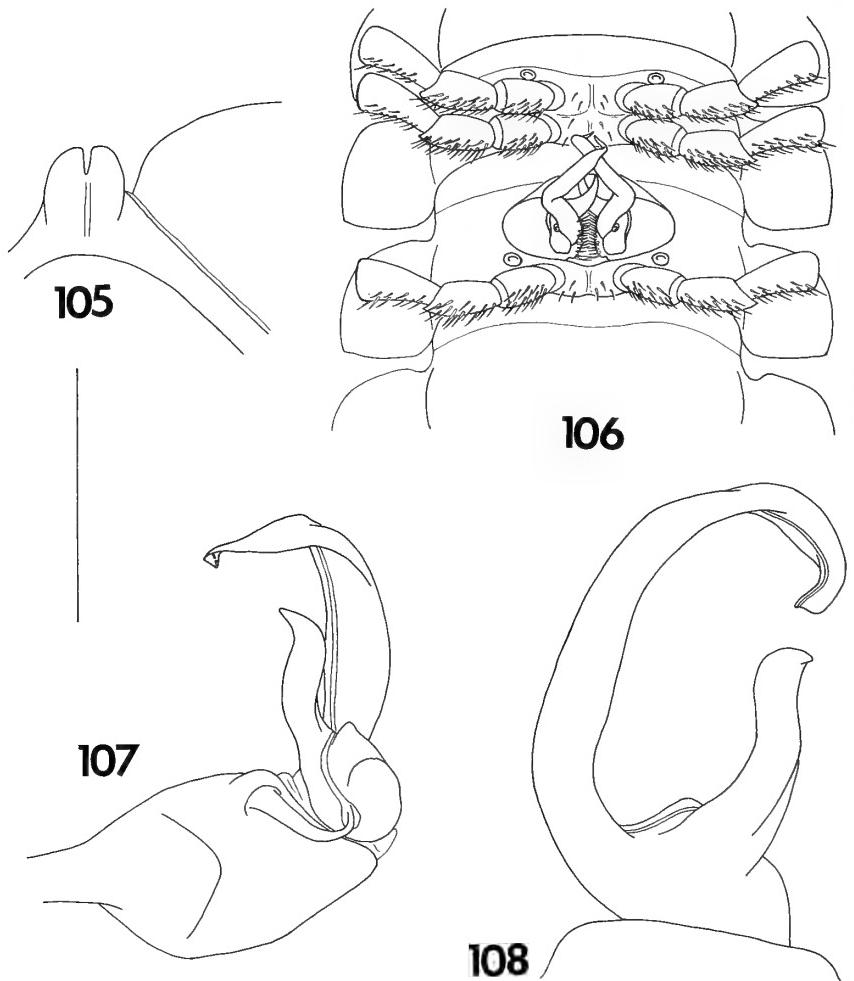
FIGS. 105-108. *Sigmoria (Falloria) picapa.* 105, process of 4th sternum of paratype, caudal view. 106, gonopods *in situ,* ventral view of topotype. 107, left gonopod of paratype, medial view. 108, telopodite of the same, lateral view. Scale line for fig. 106 = 1.00 mm; line for other figs. = 1.00 mm for 108; 1.33 mm for 105; 1.78 mm for 107.

paratype (RLH) taken by same collector, 2 June 1952, at Burrville, Morgan County. One male and one female topotypes (NCSM A3363) collected by R.M. Shelley and M.S. Morgan, 22 July 1980, from Morgan Co., 2.3 mi. NNE Sunbright, along US hwy. 27, 0.5 mi. N jct. co. rd. 2438. The male holotype apparently is missing from the NMNH, where Keeton (1960) reported its deposition. Two loan requests to this institution failed to produce it, and its location is unknown.

Diagnosis. — A large species of *Sigmoria* with medial flange running between distal extremities of basal zone and peak and with red paranota and blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process long, widest basally, tapering distad, bisinuately curved; acropodite moderately thick and heavy, arch an inverted L, extending to level of prefemoral process; basal zone long, gently curved; anterior bend well defined; peak flattened, angling slightly downward, narrowing distad; apical curve poorly defined; distal zone short, directed laterad and coplanar with peak, obscured by latter in medial view, narrowing distad and expanding into blunt tip; medial flange broadest distad; lateral flange located on peak opposite medial flange.

Color in Life. — Paranota red; metaterga black with wide blue stripes along caudal margins connecting paranotal markings; collum with red and blue stripes along anterior and posterior edges, respectively.

Male Paratype from Sunbright. — Length 42.9 mm, maximum width 10.4 mm, W/L ratio 24.2%, depth/width ratio 60.6%. Segmental widths as follows:

collum	7.5 mm	14th	10.2
2nd	8.7	15th	9.7
3rd	9.6	16th	8.9
4th-7th	10.0	17th	7.8
8th-13th	10.4	18th	6.0

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 5.1 mm, interantennal isthmus 1.9 mm. Antennae reaching back to caudal edge of 3rd paranota; relative lengths of antennomeres 2>3>6>5>4>1>7. Genae with flat central impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, clypeal about 12-12, labral about 16-16.

Dorsum smooth, polished, moderately coriaceous on paranota. Collum broad, ends extending slightly beyond those of adjacent tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 6, blunt on 7-11, becoming progressively more acute caudally. Peritremata thick and distinct, sharply elevated above paranota, ozopores located near middle of peritremata, opening dorsolaterad.

Process of 4th sternum apically divided, shorter than widths of adjacent coxae (Fig. 105); knobs of 5th sternum coalesced medially into ventrally directed process, shorter than widths of adjacent coxae, flattened areas between 5th legs distinct and subconical; sternum of segment 6 convexly depressed between 7th legs to accommodate apical curvatures of acropodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna flattened and plate-like, with bicruciform impressions on segments 8-10 and variably wide, shallow, central depressions on

remaining segments. Coxae with blunt tubercles on segments 9-15; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture ovoid, 3.3 mm wide and 1.8 mm long at midpoint, strongly indented anteriomediad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 106, of topotype) with acropodites angling anteriomediad and overlapping each other in midline of aperture, extending forward beyond anterior margin and inserting in depression between 7th legs. Gonopod structure as follows (Figs. 107-108): Prefemoral process long, wide, and bisinuately curved, about half as long as basal zone, tapering smoothly and continuously to subacuminate tip, latter directed toward distal zone. Acropodite moderately thick and heavy, blade like, becoming progressively thinner and narrower beginning at anterior bend, configuration an inverted L; basal zone long, gently curved anteriad; anterior bend sharp, well defined; peak flattened, angling slightly downward, distal half narrowing strongly; apical curve broad, poorly defined; distal zone short, curving directly laterad, coplanar with peak and obscured in medial view, narrowing slightly distad and expanding apically into blunt tip; latter bent slightly downward from distal zone, with produced inner corner resembling inverted reflexed condition. Medial flange arising on distal extremity of basal zone, extending across anterior bend and terminating on distal extremity of peak, broadest distad. Lateral flange arising on peak and terminating at same position as medial flange. Prostatic groove running along inner surface of basal zone, crossing to lateral side at anterior bend and continuing to opening on inner corner of tip.

Female Paratype. — Length 46.7 mm, maximum width 10.8 m, W/L ratio 23.2%, depth/width ratio 67.6%. Agreeing closely with males in somatic features, except ends of collum not produced beyond those of following tergite. Cyphopods *in situ* with openings of valves visible in aperture. Receptacle small, flat, located beneath medial corners of valves, surface finely granular. Valves large, equal, with broad central depression, surfaces finely granulate.

Variation. — No differences are apparent between the topotype and the described paratype. In the male from Burrville the prefemoral process is a little narrower and the basal zone straighter, but otherwise it agrees with that from Sunbright.

Ecology. — Keeton (1960) gave no indication of habitat in his description, but the topotypes I collected were found under deep piles of oak leaves in shallow ravines. There are no cove habitats or rhododendron at this site or at Burrville, and investigations in such environments near Wartburg, Oakdale, and Frozen Head State Park yielded an abundance of *Brachoria* but none of *picapa*. Thus, *picapa* is not a cove species and has different ecological preferences.

Distribution. — Known only from the type and paratype localities near Sunbright and Burrville in the Cumberland Plateau of northern Morgan County, Tennessee.

Remarks. — Although the paranota of males continue the slope of the dorsum and can be described as moderately depressed, they angle more sharply ventrad than in most congeners. Males of *picapa* thus appear thicker and more highly arched or vaulted than most *Sigmoria* males.

The medial view of the gonopod (Fig. 107) was prepared from more anterior and dorsal angles than usual to show the tip, which is coplanar with

the peak and obscured by the latter in strictly medial perspective. The acropodite therefore appears to extend well beyond the level of the prefemoral process, but it really does not as shown in lateral view (Fig. 108). Although they are over 80 miles and two physiographic regions apart, the configuration of the prefemoral process of *picapu* more closely resembles that of *prolata* than those of any other Cumberland species.

I visited the type locality twice in 1979 and once in 1980 with my assistants to search for topotypical males. They were harder to find than any other species of *Sigmoria s. lat.*, and around 40 man hours were required for the two specimens, which were finally discovered on the third trip. Investigations north of the known area in Fentress and Scott counties and the adjacent part of Kentucky were unproductive, although there is an abundance of ostensibly desirable sites.

The *Mimetica* Group

With three species in the Nashville Basin and the eastern Highland Rim of central Tennessee, the *mimetica* group forms the western distributional limit of *Sigmoria s. lat.* The species have thick, sturdy acropodites, and next to *rileyi* and *abbotti, crassicurvosa* and *pendulata* have the most massive in the genus. The telopodite is oriented differently on the coxa, so that the inner surface of the basal zone is directed mediad instead of anteriomediad, and the peak is also tilted laterad exposing the undersurface in medial view. Because of these changes, the prostatic groove is visible in medial view from its origin on the prefemur to the apical curve or distal zone. The lateral flange is absent and the medial flange appears to be also, but I think it is represented by a slightly wider margin along the peak that is inconspicuous in medial view because of the tilting. It can be seen in a ventral examination of the peak but is poorly demarcated from the acropodite stem, and its origin and termination are indistinct. In the interests of consistency, I report it as located on the peak. Prefemoral processes are generally short to vestigial. Color hues are lighter than those of the Cumberland and Appalachian species. Red is replaced by pink, and the blue stripes are lighter with less of a grayish tint than occurs in other species.

Components. — *mimetica* (Chamberlin); *crassicurvosa,* new species; *pendulata,* new species.

Sigmoria (Falloria) mimetica Chamberlin   Figs. 109-114

Fontaria mimetica Chamberlin, 1918a:29-30. Attems, 1938:167.
Sigmoria mimetica: Hoffman, 1950:6. Chamberlin and Hoffman, 1958:51.
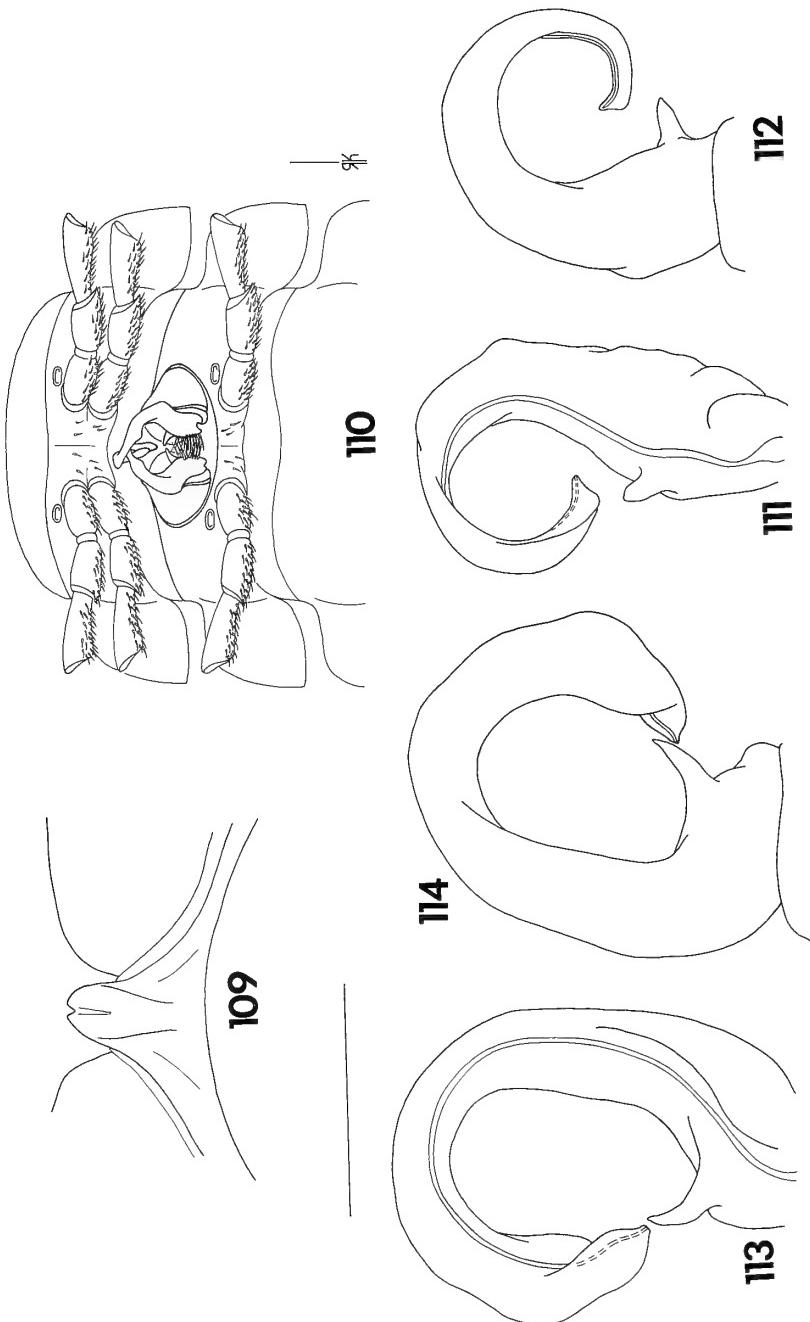
Type specimens. — Male holotype (RVC) collected by H. Cummins, 21 April 1917, from Glendale Hills south of Nashville, Davidson Co., TN. Hoffman (1950) and Chamberlin and Hoffman (1958) report that the type is in the MCZ collection, but it currently is located in the RVC. There is no section of Nashville by this name, but according to the Chamber of Commerce, it probably refers to the area near Glendale Lane and the communities of Oak Hill and Forest Hills in south Nashville. This area, just north of the Williamson County line, contains Lake Radnor State Park, and the specimens from there are considered topotypes.

Diagnosis. — A moderate-size species of *Sigmoria* with narrow medial flange located on peak and with pink paranota and usually blue metatergal stripes; gonopods with following diagnostic characters: acropodite moderately thick and heavy, arch high and rounded, extending beyond level of prefemoral process; basal zone with inner surface directed mediad, with small, rounded distomedial lobe; anterior bend and apical curve poorly defined; peak tilted laterad, exposing undersurface in medial view; distal zone long, curving broadly into arch and extending nearly to proximal part of basal zone, coplanar with latter, twisted near midlength; tip blunt, located on inner corner of distal zone; medial flange narrow and inconspicuous in medial view, located on peak, with small, rounded distal lobe; lateral flange absent.

Color in Life. — Paranota pink; metaterga black, with blue (occasionally white) transverse stripes along caudal margins connecting paranotal spots; collum with or without concolorous blue or white stripe on anterior edge.

Holotype. — Body fragmented, see topotype description for measurements.

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.5 mm; interantennal isthmus 1.8 mm. Antennae reaching back to middle of third paranota; relative lengths of antennomeres 2>3>4=6=5>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial, interantennal, and frontal absent, clypeal about 10-10, labral about 12-12, merging with clypeal series and continuing for short distances along genal margins.

Terga smooth, polished, with only faint wrinkling. Collum broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded on collum but moderately acute thereafter. Peritremata low on anterior segments, becoming sharp and distinct in midbody region. Ozopores located in caudal half of peritremata, opening dorsad.

Fig. 109-114. *Sigmoria (Falloria) mimetica.* 109, process of 4th sternum of holotype, caudal view. 110, gonopods *in situ,* ventral view of topotype. 111, telopodite of left gonopod of holotype, medial view. 112, the same, lateral view. 113, telopodite of left gonopod of male from 11 mi. E. Lebanon, Wilson Co., TN, medial view. 114, the same, lateral view. Scale line for fig. 110 = 1.00 mm; line for other figs. = 1.00 mm for 113-114; 1.33 mm for 109; 1.78 mm for 111-112.

Process of 4th sternum shorter than widths of adjacent coxae and divided apically (Fig. 109); of segment 5, produced into pair of small, paramedial knobs between 4th pair of legs and lower, more rounded lobes between 5th legs; of segment 6, convexly recessed between both leg pairs to accommodate gonopodal acropodites. Postgonopodal sterna relatively flat, with shallow transverse grooves originating between leg pairs. Coxae without ventrodistal spines or tubercles on all legs; prefemoral spines beginning on segment 6, becoming longer and sharper caudally.

Gonopodal aperture rounded, 3.1 mm wide and 2.1 mm long at midpoint, without indentations on anteriolateral margins, sides flush with metazonal surface, caudal margin slightly thickened. Gonopods *in situ* (Fig. 110, of topotype), with acropodites curving anteriomediad over aperture, overlapping and bending abruptly dorsad apically, extending beyond anterior margin of aperture to between 7th legs. Gonopod structure as follows (Figs. 111-112): Prefemur with short prefemoral process directed toward distal zone of acropodite, sides parallel, tapering apically to central tip. Acropodite moderately thick and heavy, arch high and rounded, overhanging and extending well beyond level of prefemoral process; basal zone relatively long and broad, situated with inner surface directed mediad, with small, rounded distomedial lobe; anterior bend broad, poorly defined; peak relatively short, high and rounded, tilted laterad exposing undersurface in medial view; apical curve broad, poorly defined; distal zone long, coplanar with basal zone, curving broadly into arch, extending nearly to base of acropodite just above level of prefemoral process and directed toward basal zone, twisted slightly near midlength producing additional surface on medial side; tip subacuminate, located on inner corner of distal zone, suggesting reflexed condition. Medial flange narrow and inconspicuous, located on peak but possibly incorporating lobe on basal zone. Lateral flange absent. Prostatic groove running along inner surface of acropodite, entirely visible in medial view until reaching distal zone.

Male Topotype. — Length 36.2 mm, maximum width 9.6 mm, W/L ratio 26.5%, depth/width ratio 46.9%. Segmental widths as follows:

collum 7.1 mm	13th 9.2
2nd 8.0	14th 9.0
3rd 8.9	15th 8.5
4th 9.2	16th 7.0
5th-7th 9.4	17th 6.6
8th-12th 9.6	18th 4.9

The topotypes agree closely with the holotype in somatic and gonopodal features. The only noticeable difference is that the prefemoral process is slightly longer.

Female Topotype. — Length 36.0 mm, maximum width 9.3 mm, W/L 25.8%, depth/width 65.6%. Agreeing closely with holotype in somatic features, except ends of collum not produced beyond those of following segment. Cyphopods *in situ* with corners of receptacles visible in aperture, valves directed anteriolaterad. Receptacle large, situated along bases of valves, surface rugulose but smooth. Valves moderate and equal, surfaces finely granulate.

Variation. — The gonopods of *mimetica* are quite uniform. The length of the prefemoral process varies and the arch may be broader than in the holotype, but these minor differences occur randomly throughout the range. On the eastern edge of the range, 11 mi. E Lebanon, Wilson County, occurs the different form shown in figures 113-114. The prefemoral process tapers smoothly and continuously throughout the length, rather than just apically, and the acropodite has rounded lobes on the lateral margin at the

apical curve and another one just proximal to the tip, which is blunt. The distal zone is directed toward the prefemoral process instead of the basal zone. I believe it is a relict of a former faunal connection between *mimetica* and *crassicurvosa,* and it may be extinct, as this area has been examined three additional times without success. Since it occurs on the range periphery of *mimetica,* I include it under this species.

Ecology. — I have taken *mimetica* under thin layers of leaves on relatively hard substrates near water sources. Some samples, for example those in Henry Horton and Cedars of Lebanon State Parks, were remote from water but still met the other ecological criteria.

Distribution. — An area about 60 miles long and 50 miles wide in the Nashville Basin and adjacent fringe of the Western Highland Rim of central Tennessee. All specimens have been taken north of the Duck River, and the range traverses the Cumberland River. I have not encountered *mimetica* in the Eastern Highland Rim Province or in Kentucky, although the Robertson and Macon County localities are only about 10 miles south of the state line. Specimens were examined as follows:

TENNESSEE. — *Robertson Co.,* 3 mi. E Springfield, along TN hwy. 76, 2.2 mi. E jct. TN hwy. 49, M, F, 12 June 1979 (NCSM A2753). *Summer Co.,* 1.7 mi. S. Bransford, 3M, 3F, 20 April 1958, L. Hubricht (RLH). *Macon Co.,* 4 mi. SW Lafayette, 2M, F, 26 April 1958, L. Hubricht (RLH). *Cheatham Co.,* 3.6 mi. N Ashland City, along TN hwy. 49, 3.6 mi. N jct. TN hwy. 12, 4M, 6F, 12 June 1979 (NCSM A2758). *Davidson Co.,* 6 mi. SE Ashland City, along TN hwy. 12 at Cheatham Co. line, 2F, 12 June 1979 (NCSM A2759); Glendale Hills S Nashville, M, 21 April 1917, H. Cummins (RVC) TYPE LOCALITY; and Lake Radnor St. Pk., 6M, 2F, 12 June 1979 (NCSM A2761). *Wilson Co.,* 11 mi E Lebanon, 2M, 25 June 1957, L. Hubricht (RLH); 12.8 mi. NNE Lebanon, along US hwy. 70N, 0.8 mi. W Smith Co. line, M, 2F, 28 May 1980 (NCSM A3167); and Cedars of Lebanon St. Pk., 10M, 3F, July 1958, R.M. Sinclair (RLH) and 3M, 16 June 1976 (NCSM A876). *Cannon Co.,* 5.0 mi. NW Woodbury, along TN hwy. 145, 4.8 mi. N jct. US hwy. 70S, 4M, 3F, 9 May 1979 (NCSM A2653). *Williamson Co.,* "beyond Glendale," M, 14 October 1916, H. Cummins (RVC). *Maury Co.,* 6.3 mi. ENE Columbia, along TN hwy. 99, 5.5 mi. E jct. US hwy. 31, M, 10 May 1979 (NCSM A2662). *Marshall Co.,* Henry Horton St. Pk., campground area, 12M, 8F, 9 May 1979 (NCSM A2660).

Remarks. — In addition to the holotype, Chamberlin (1918a) also reported a female of *mimetica* from Hillsboro Hills, Nashville, and a male from "beyond Glendale." Both are present in the Chamberlin collection, but the female could be of *Brachoria glendalea* (Chamberlin), which is sympatric with *mimetica* in southern Davidson County. Since the area thought to represent Glendale Hills touches the Williamson County line, the male from "beyond Glendale" is considered to be from this county and is so cited above.

Sigmoria (F.) mimetica is the westernmost species in the genus, and the collection from Cheatham County, specifically, constitutes the range limit.

I have sampled intensively over 40 miles farther west to the Tennessee River, and sporadically another 85 or so miles to the Mississippi River, to confirm that no congeners exist in this direction.

Sigmoria (Falloria) crassicurvosa Shelley, new species   Figs. 115-120

Type specimens. — Male holotype (NCSM A2750) and 2 male and 3 female paratypes collected by R.M. Shelley and R.K. Tardell, 11 June 1979, from Smith Co., TN, 2.0 mi. W Carthage, along TN highway 25, 1.2 mi. W junction with TN highway 85. Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* with narrow medial flange located on peak and with pink paranota and blue transverse metatergal stripes; gonopods with following diagnostic characters: prefemoral process variable, short and acute or vestigial; acropodite thick and massive, broadly curved and subtending rectangular arch, extending well beyond level of prefemoral process; basal zone with inner surface directed mediad, with or without ledge on medial surface; anterior bend and apical curve sharp, well defined; peak gently curved, tilted laterad, exposing undersurface in medial view, with or without distal expansion on lateral surface; distal zone equal in length to and coplanar with basal zone, either parallel to latter and bent into arch near midlength or angling into arch, configuration variable, with or without proximal indentation on lateral surface, broadly rounded lobe at midlength on medial side, and terminal medial lamina; tip elongated and acuminate, with converging striae.

Color in life. — Paranota pink; metaterga black with blue transverse stripes along caudal margins connecting paranotal spots; collum with concolorous blue stripes along anterior and posterior edges.

Holotype. — Length 36.2 mm, maximum width 9.0 mm, W/L 24.9%, depth/width ratio 53.2%. Segmental widths as follows:

collum 6.4 mm	15th 8.7
2nd 7.8	16th 7.9
3rd 8.5	17th 6.8
4th 8.9	18th 5.3
5th-14th 9.0	

Figs. 115-120.   *Sigmoria (Falloria) crassicurvosa.*   115, process of 4th sternum of holotype, caudal view.   116, gonopods *in situ,* ventral view of paratype.   117, telopodite of left gonopod of holotype, medial view.   118, the same, lateral view.   119, the same, subdorsal view.   120, telopodite of left gonopod of male from Dekalb Co., TN, medial view. Scale line for fig. 116 = 1.00 mm; line for other figs. = 0.80 mm for 119; 1.00 mm for 117-118 and 120; 1.33 mm for 115.
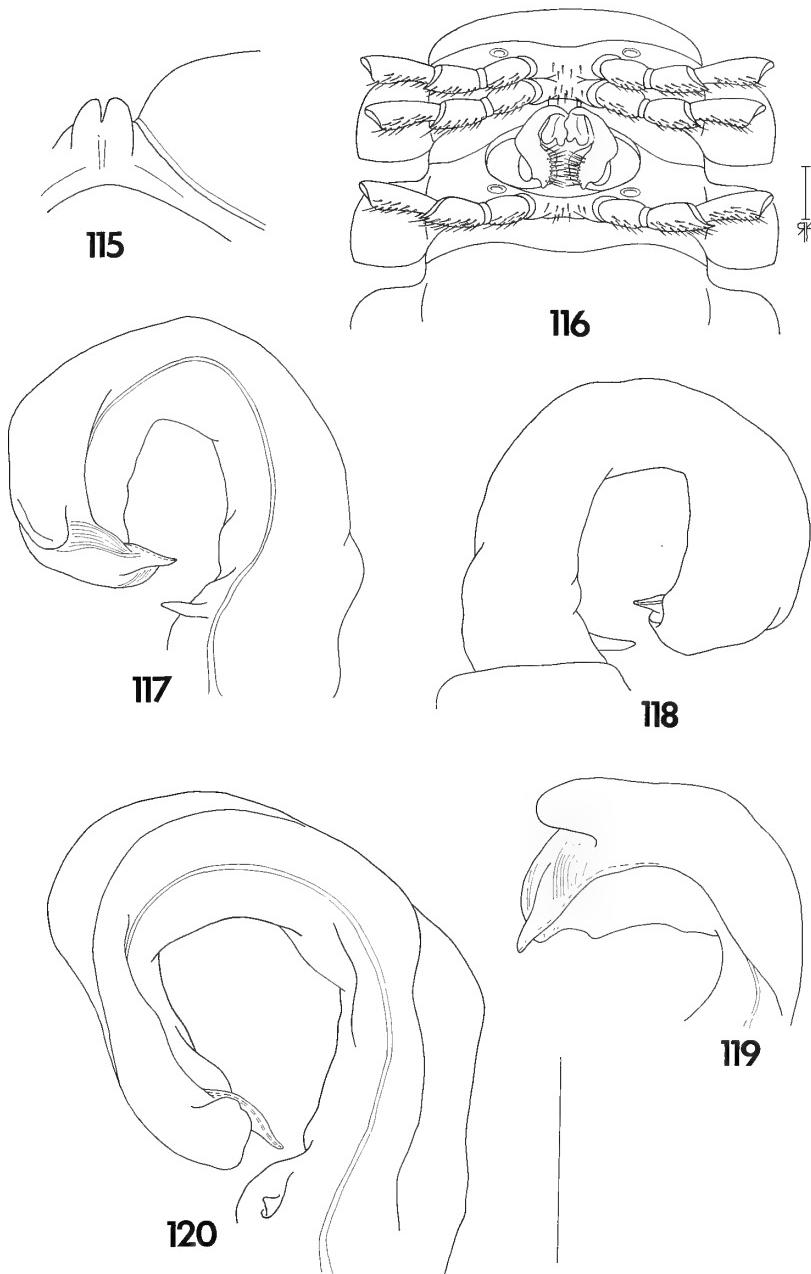
115

116

117

118

119

120

Somatic features similar to *l. latior*, with following exceptions:

Width across genal apices 4.4 mm, interantennal isthmus 1.3mm. Antennae reaching back to middle of 3rd paranota, relative lengths of antennomeres $2 > 3 > 4 = 5 > 6 > 1 > 7$. Genae with distinct impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal about 10-10, labral 12-12.

Terga smooth, polished, becoming moderately coriaceous on paranota. Collum broad, ends not produced beyond those of following tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 5, blunt on 6-12, becoming progressively more acute posteriorly. Peritremata flat on anterior segments, becoming elevated and distinct on segment 6. Ozopores located near middle of peritremata, opening dorsad.

Sternum of segment 4 with small, divided process, much shorter than widths of adjacent coxae (Fig. 115); that of segment 5 with two conical paramedian knobs between 4th legs, much shorter than adjacent coxal widths, and two low elevated areas between 5th legs; that of segment 6 strongly and convexly depressed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna flattened and platelike, with bicruciform impressions on segments 8-9 and shallow central impression thereafter. Coxae with low, rounded tubercles on segments 10-12; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 4.0 mm wide and 1.3 mm long at midpoint, without indentations, sides flush with metazonal surface. Gonopods *in situ* (Fig. 116, of paratype) with acropodites curving anteriad entirely over aperture, angling slightly toward midline and touching or slightly overlapping in apical curve regions. Gonopod structure as follows (Figs. 117-119): Prefemoral process short and acute, directed towards coxa. Acropodite thick and massive, heavily sclerotized, broadly curved but subtending rectangular arch, overhanging and extending well beyond level of prefemoral process; basal zone with inner surface directed mediad, relatively long and straight, without modifications; anterior bend sharp, well defined; peak relatively long, gently curved, tilted laterad exposing undersurface in medial view; apical curve sharp, well defined; distal zone long, equal in length and coplanar with basal zone, with broadly rounded lobe distad on medial side, bent inward into arch apically; tip broadly rounded on lateral side, with striae on both lateral and medial sides converging onto elongated, acuminate medial corner. Medial flange narrow and indistinct, located on peak. Lateral flange absent. Prostatic groove running along medial and inner surfaces of acropodite to terminal opening.

Male paratypes. — The male paratypes agree with the holotype in all particulars.

Female paratype. — Length 42.5 mm, maximum width 10.1 mm, W/L 23.8%, depth/width ratio 64.4%. Cyphopods *in situ* with corners of valves and receptacles visible in apertures, valves directed anteriolaterad. Receptacle large, situated along bases of valves, surface rugulose but smooth. Valves moderate and equal, surfaces finely granulate.

Variation. — The Dekalb County males differ considerably from the types as shown in figure 120. The prefemoral process is a vestigial nub and barely detectable on the massive prefemur. There is a ledge along the medial surface of the basal zone that is broadest distad and might represent part of the medial flange. The peak is expanded distad into a rounded lateral margin, which is indented on the proximal part of the distal zone. This section of the acropodite is straight and angles toward the basal zone instead of being parallel as in the holotype. Apically, there is no medial lobe on the distal zone, but there is a terminal lamina which obscures the proximal part of the solenomerite in medial view.

Ecology. — Sigmoria (F.) crassicurvosa occurs under thin layers of .ves on relatively hard substrates near water sources.

Distribution. — Known only from the following three localities on the ;tern edge of the Nashville Basin.

`ENNESSEE. — *Smith Co.,* 2 mi. W Carthage, along TN hwy. 25, 1.2 mi. W jct. TN hwy. 3M, 3F, 11 June 1979 (NCSM A2750) TYPE LOCALITY; and 7 mi. SW Carthage, along 1umbered rd. off TN hwy. 141, M, F, 28 May 1980 (NCSM A3170). *Dekalb Co.,* 5 mi. ᴎW Smithville, along US hwy. 70, 3M, 9 May 1979 (NCSM A2648).
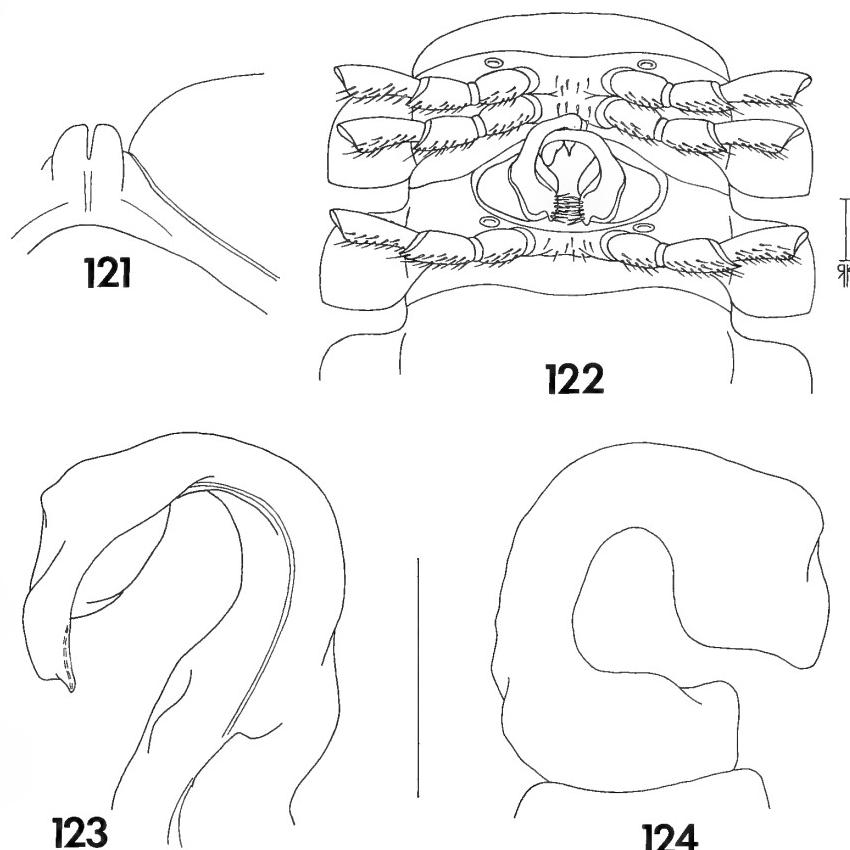
Figs. 121-124. *Sigmoria (Falloria) pendulata.* 121, process of 4th sternum of holotype, caudal view. 122, gonopods *in situ,* ventral view of paratype. 123, telopodite of left gonopod of holotype, medial view. 124, the same, lateral view. Scale line for fig. 122 = 1.00 mm; line for other figs = 1.00 mm for 123-124; 1.33 mm for 121.

Sigmoria (Falloria) pendulata Shelley, new species   Figs. 121-124

Type specimens. — Male holotype (NCSM A2650) and 5 male and 5 female paratypes collected by R.M. Shelley and R.K. Tardell, 9 May 1979, from Edgar Evins State Park, Dekalb Co., TN. Male and female paratypes deposited in FSCA.

Diagnosis. — A moderate-size species of *Sigmoria* with medial flange on peak and with pink paranota and usually blue metatergal stripes; gonopods with following diagnostic characters: prefemoral process absent or varying in size to moderately long and acute; acropodite thick and massive, arch an
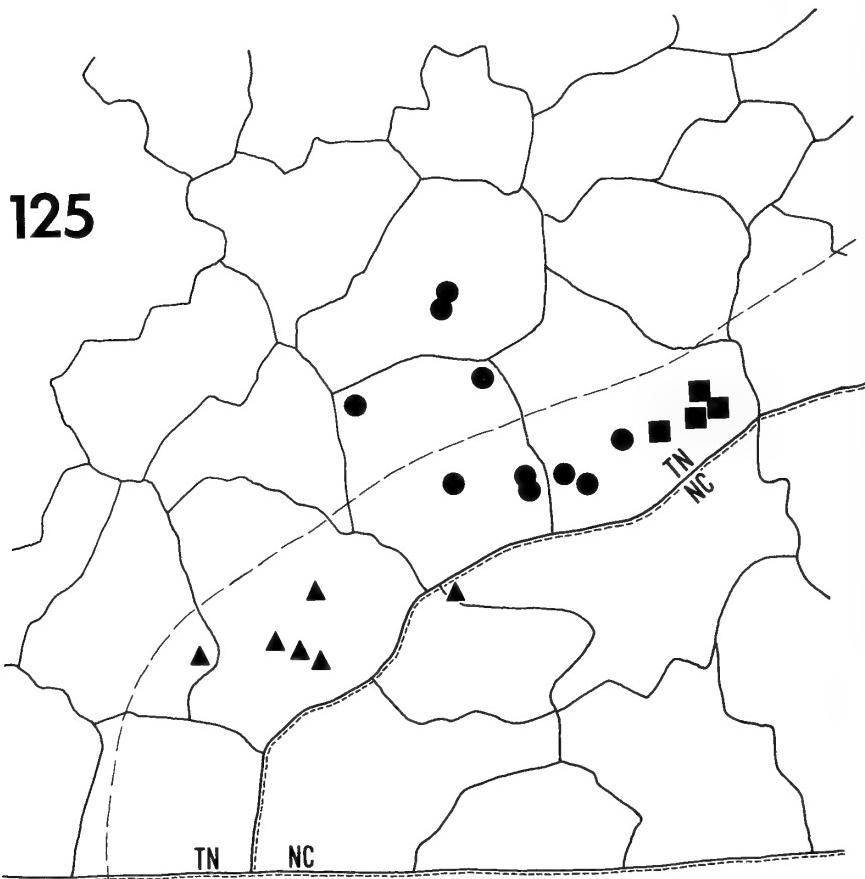
FIG. 125.   Distributions of *ainsliei,* dots; *aphelorioides,* triangles; and *prolata,* squares, in western North Carolina and eastern Tennessee. The dashed line is the approximate boundary between the Blue Ridge and Ridge and Valley Provinces.

inverted U, extending well beyond level of prefemoral process; basal zone with inner surface directed mediad; anterior bend and apical curve well defined; peak high and rounded, tilted laterad; distal zone coplanar with and equal in length to basal zone, with expansion at midlength on anterior side extending onto medial and lateral surfaces and forming lobes, curved slightly inward distad and tapering to blunt tip.

Color in Life. — Paranota pink; metaterga black with blue, occasionally yellow, stripes along caudal margins connecting paranotal spots; collum with pink stripe along anterior edge and blue along posterior.

Holotype. — Length 33.9 mm, maximum width 9.0 mm, W/L ratio 26.5%, depth/width ratio 69.7%. Segmental widths as follows:

collum 6.4 mm	8th-14th 9.0
2nd 7.6	15th 8.5
3rd 8.3	16th 8.0
4th 8.5	17th 6.5
5th-7th 8.8	18th 4.6

Somatic features similar to *l. latior,* with following exceptions:

Width across genal apices 4.7 mm, interantennal isthmus 1.4 mm. Antennae reaching back to caudal edge of 3rd paranota, relative lengths of antennomeres 2>3>6>4>1>7. Genae with shallow central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, frontal 1-1, clypeal 12-12.

Terga smooth, polished, with only faint wrinkling on anterior parts of paranota. Collum broad, ends extending slightly beyond those of adjacent tergite. Paranota moderately depressed, continuing slope of dorsum, caudolateral corners rounded through segment 5, blunt on 6-12, becoming progressively more acute posteriorly. Peritremata sharp and distinct on all segments, clearly elevated above metazonal surface, ozopores located near middle of peritremata, opening dorsolaterad.

Sternum of segment 4 with minute, divided projection, much shorter than adjacent coxal widths (Fig. 121); that of segment 5 with two low rounded knobs between 4th legs, much shorter than adjacent coxal widths, and broad flattened elevations between 5th legs; that of segment 6 deeply and convexly recessed between 7th legs to accommodate apical curvatures of acropodites. Postgonopodal sterna flattened and plate-like, bicruciately impressed on segments 8-9 and with variably broad, shallow central impressions on remaining segments. Coxae with low rounded tubercles beginning on segment 8; prefemoral spines beginning on segment 5, becoming progressively longer and sharper caudally.

Gonopodal aperture elliptical, 3.5 mm wide and 1.8 mm long at midpoint, without indentations, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 122, of paratype) with acropodites extending anteriomediad and peak of one overlapping apical curve of other, apical curve of former extending slightly beyond anterior margin of aperture and inserting in depression between 7th legs. Gonopod structure as follows (Figs. 123-124): Prefemoral process absent, with only a lowly rounded ridge at this position on prefemur. Acropodite thick and massive, heavily sclerotized, subtending symmetrical, inverted U shaped arch, overhanging and extending well beyond prefemur; basal zone moderately long, inner surface directed mediad; anterior bend sharp, well defined, continuous through peak with distal zone; peak short, high, and rounded, apex at midlength, continuing curvature of arch, tilted only slightly laterad; apical curve sharp, well defined; distal zone long, coplanar with and nearly equal in length to basal zone, with broadly rounded swelling at midlength on anterior side extending

onto medial and lateral surfaces thus producing lobe-like effect at this point, slightly curved beyond swelling and tapering to blunt termination, directed toward cannula of coxa; tip located on produced inner corner of distal zone. Medial flange narrow, located on peak, indistinct in medial view. Lateral flange absent. Prostatic groove running along inner surface of basal zone and under surface of peak to opening at tip of distal zone.

Male Paratypes. — The male paratypes agree with the holotype in all structural details. In color, however, four specimens had yellow metatergal stripes as opposed to the blue stripes of the holotype and one paratype.

Female Paratype. — Length 37.9 mm, maximum width 10.3 mm, W/L ratio 27.2%, depth/width ratio 67.9%. Cyphopods *in situ* with corners of valves and receptacles visible in apertures, valves directed anteriolaterad. Receptacle large, situated along bases of valves, surface rugulose but smooth. Valves moderate and equal, surfaces finely granulate.

Variation. — Color varies only in the type series. All other specimens have blue metatergal stripes connecting pink paranotal markings.

Males in the eastern edge of the range in Putnam County possess long, acute prefemoral processes that extend nearly to the levels of the distal
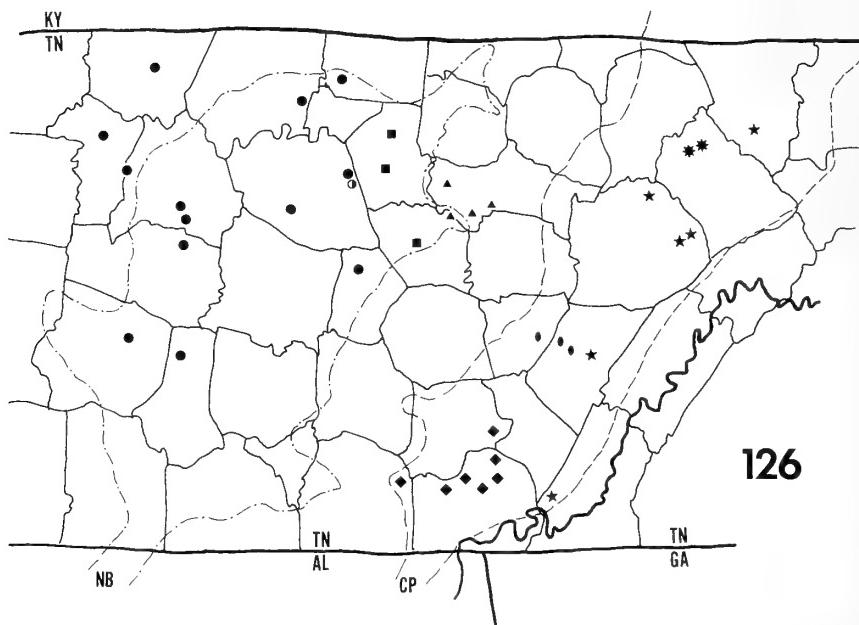
FIG. 126. Distribution of the subgenus *Falloria* in central Tennessee. Dots, *mimetica;* half shaded dot, atypical population, possible remnant of intergrades between *mimetica* and *crassicurvosa;* squares, *crassicurvosa;* triangles, *pendulata;* asterisks, *picapa;* stars, *forficata,* ovals, *abbreviata;* diamonds, *houstoni.* The dashed lines show the approximate boundaries of the Cumberland Plateau Province (CP), and the Nashville Basin (NB) is denoted by a line of alternating dots and dashes. The intervening area, which curves northward over the Nashville Basin and continues on the western side, is the Highland Rim. The heavy line in the southeastern (lower right) corner represents the course of the Tennessee River.

zones, and there is a geographic trend toward a longer and larger structure from west to east. The types and the most proximal sample from western Putnam County lack the process, and it is short but distinct in sample A3176, from an intermediate locality. However, no changes are evident in the acropodites.

Ecology. — *Sigmoria (F.) pendulata* occurs under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — Known only from an area about 13 miles long and 8 miles wide in the eastern Highland Rim. Specimens were examined as follows:

TENNESSEE. — *Dekalb Co.,* Edgar Evins St. Pk., 6M, 5F, 9 May 1979 (NCSM A2650-2651) TYPE LOCALITY. *Putnam Co.,* 12 mi. W Cookeville, along US 70N at Lafayette Twp., 2M, 7F, 10 June 1979 (NCSM A2748); 14.3 mi. SW Cookeville, along co. rd. 6162, 0.3 mi. S TN hwy. 141, 5M, 4F, 28 May 1980 (NCSM A3176); and 9.5 mi. SSW Cookeville, Burgess Falls area on Falling Water Rd., 3M, 2F, 29 May 1980 (NCSM A3178).

Remarks. — Approximately 17 miles separate the ranges of *pendulata* and *mimetica,* and if the swelling on the distal zone of *pendulata* were removed, its acropodite would be very close to that of the latter except for slightly less curvature in the distal zone.

PART II: REVISION OF DELTOTARIA
by Rowland M. Shelley

Taxonomic Characters

Hoffman (1961) cited two diagnostic features for *Deltotaria,* the coxal apophysis and the absence of frontal and vertigial (epicranial) facial setae. However, many apheloriine xystodesmids lack epicranial setae, and with much more material at my disposal, I can report that frontal setae are present on most individuals of both sexes of *Deltotaria.* Thus, the only truly diagnostic generic character is the subconical coxal apophysis. Hoffman also reported that the gonocoxae were connected by a partially sclerotized sternal remnant, which would be a second such feature as this was one of the traits cited for the tribe Rhysodesmini (Hoffman 1960). However, I have carefully examined a number of males of both species and found that although the membrane joining the coxae is occasionally quite tough and difficult to tear, there is no evidence of sclerotization. *Deltotaria* thus conforms to contribal genera in lacking a sternal remnant. Hoffman also regarded the form of the caudolateral corner of the paranota as significant at the specific level, since the peritremata are prolonged slightly beyond the

caudal edge in some forms to produce a small projection. However, this occurs widely in the Apheloriini and is insignificant. As with most apheloriine genera, the taxonomically important characters in *Deltotaria* involve chiefly the male gonopods. The two species are differently colored, as indicated below, but the pregonopodal sternal processes are nearly identical and insufficiently different from conditions in sympatric species to be useful in generic determinations.

Coloration. — Both species exhibit the metatergal stripe pattern characteristic of many forms of *Sigmoria s. lat.,* but *lea* Hoffman, in the Piedmont Plateau, is exclusively yellow, whereas *brimleii* Causey, in the southern Blue Ridge Province, displays various shades of red and orange. There is also an unusual aspect to the colors of *lea* and southern specimens of *brimleii philia* (Chamberlin) that was first reported by Filka and Shelley (1980). Whereas many xystodesmids display a glossy, highly polished finish, there is a sparkle or glitter to the pigments of these forms of *Deltotaria* that is much like that of metallic paint. This sheen of *lea* allows for positive identifications of even females in the field and thus is diagnostic for both the species and the genus in the Piedmont Plateau. The difference is unmistakable and readily apparent if one compares live specimens of *D. lea* and sympatric, yellow striped intergrades of *Sigmoria (Sigmoria) latior.*

Gonopodal Characters. — In the terminology I have developed for "sigmoid" gonopods, what Hoffman (1961) labeled a subterminal lobe or process and identified by the letter "B" is really the lateral flange, and what he considered the solenomerite is actually the part of the distal zone distal to the flange. To date, all gonopodal drawings of *Deltotaria* have also been from a somewhat ventrolateral aspect since this view best reveals the coxal apophyses. Consequently, the medial flanges have yet to be illustrated or described. These lamellae clearly reveal the generic affinity between *Deltotaria* and *Sigmoria s. lat.,* and the locations are diagnostic at the specific level. I therefore present medial views of all illustrated gonopods to highlight this as yet unrevealed feature.

The coxal apophysis is the only truly diagnostic generic character, as the gonopods would otherwise be readily referrable to *Sigmoria s. lat.* This projection arises anteriolaterad on the coxa and extends directly ventrad. The length and configuration are useful at the specific level, and as viewed in medial and lateral profiles, there are two basic types — broadly triangular with sides narrowing rapidly to a subacuminate tip, and long and slender with sides roughly parallel through most of the length except apically. Triangular apophyses obtain in *lea,* where the projection is short and terminates below the level of the prefemur, and the nominate subspecies of *brimleii,* where it is moderately long and extends to the level of the

prefemoral process. In *b. philia* the process is slender and much longer, stretching to or beyond the level of the tip of the acropodite and thus well beyond the prefemoral region. Despite the clear distinctions in the coxal apophyses, I do not believe the two forms of *brimleii* are reproductively isolated, as there is evidence of intergradation and there are no significant acropodal differences.

On the acropodites, specific differences obtain in the apical thickness, the curvature of the distal zone, and the locations and shapes of the medial and lateral flanges. *Deltotaria lea* has a decidedly stronger, thicker, and heavier acropodite than does *brimleii,* particularly in the distal zone, which is broad and spatulate in the former and thin and fragile in the latter. Accordingly, *lea* is apically blunt whereas *brimleii* is subacuminate. In curvature, the distal zone extends downward from the peak in *lea* and is coplanar with the basal zone. In *brimleii,* however, the section projects laterad to varying degrees, is not coplanar with the basal zone, and in a few individuals is nearly coplanar with the peak. All forms of *Deltotaria* have a medial flange, but in *lea* it is broadly expanded and located on the basal zone, whereas in *brimleii* it is narrow and located on the peak and/or distal zone. In *lea* the flange is curved to form a concave inner surface on the basal zone. In *brimleii* the flange is level or straight with sometimes a gently rounded margin, but it is comparatively indistinct and poorly demarcated from the acropodite stem. The lateral flange is absent from *lea* and present in *brimleii,* where there is a general trend toward smaller flanges in a southerly direction. In northern populations the lateral flange is produced into lobes of varying lengths and shapes, but in *b. philia* at the southern periphery, it is narrow, indistinct, and poorly demarcated from the acropodite stem. Here, the flange imparts a hastate appearance to the acropodite and is best detected in profile by examining the distal zone from a ventral perspective.

Genus DELTOTARIA Causey

Deltotaria Causey, 1942:165. Chamberlin and Hoffman, 1958:29. Hoffman, 1961:22-25; 1979:158. Jeekel, 1971:258.
Phanoria Chamberlin, 1949:101. Jeekel, 1971:279

Type species. — Of *Deltotaria, D. brimleii* Causey, 1942, by original designation; of *Phanoria, P. philia* Chamberlin, 1949, by original designation.

Diagnosis. — Characterized by the variably triangular or elongate coxal apophysis.

Color in Life. — Paranota red, orange, or yellow; metaterga black with concolorous red, orange, or yellow stripes along caudal margins connecting paranotal spots; collum with stripes along anterior or both margins; colors sometimes with sparkling, metallic sheen.

Description. — Head of normal appearance, smooth, polished. Epicranial suture shallow, distinct, terminating in interantennal region; interantennal isthmus moderately wide; genae not margined laterally, with shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with 4 conical sensory cones on ultimate article, no other sensory structures apparent. Facial setae reduced; epicranial and interantennal absent; frontal and genal present or absent, clypeal and labral present.

Terga generally smooth, polished, becoming moderately coriaceous on anterior halves of paranota. Collum variably broad, ends extending slightly beyond those of following tergite. Paranota moderately depressed, generally continuing slope of dorsum, caudolateral corners rounded on anteriormost segments, becoming blunt in midbody region and progressively more acute posteriorly. Peritremata generally indistinct, slightly elevated above paranotal surfaces; ozopores located caudal to midlength, opening dorsolaterad. Prozonites smaller than metazonites; strictures distinct, smooth.

Caudal segments normal for family.

Sides of metazonites smooth or irregular, with varying shallow, curved impressions. Strictures sharp, distinct. Pregonopodal sterna of males modified as follows: that of segment 4 with small to moderate, apically divided process between 3rd legs, shorter than widths of adjacent coxae; that of segment 5 with small projections between anterior legs and variable elevated areas between posterior ones; that of segment 6 with variable convex recession between caudal legs to accommodate apices of acropodites when body segments compressed, 7th legs sometimes set slightly farther apart than 6th. Postgonopodal sterna generally flat and unmodified, with shallow grooves on those immediately posterior to 7th segment and shallow central impressions on rest. Gonapophyses on 2nd leg pair of males distinctly elevated above coxal surfaces, with round, apical knobs. Pregonopodal legs densely hirsute; postgonopodal legs becoming progressively less hirsute caudally. Coxae with low tubercles beginning on postgonopodal legs, becoming progressively longer and sharper caudally; prefemoral spines beginning on segment 5, becoming longer and more acute caudally; tarsal claws bisinuate. Hypoproct variable, subtriangular to rounded; paraprocts with margins strongly thickened.

Gonopodal aperture ovoid to elliptical, with slight indentation anteriolaterad, front flush with metazonal surface, sides and caudal edge elevated. Gonopods *in situ* with acropodites projecting ventrad from aperture, curving anteriomediad and overlapping at various positions in midline, extending anteriad slightly beyond anterior margin of aperture. Coxae moderate, connected by membrane only, no sternal remnant, with subconical apophyses of variable lengths arising on anterior sides and projecting ventrad. Telopodite set terminally on coxa, latter not projecting distad beyond prefemoral region. Prefemora moderate, with or without variable prefemoral processes, latter occasionally vestigial. Acropodite moderately thick and heavy basally, becoming thinner and more fragile or spatulate distally, with torsion, curving through one or more vertical planes in vaguely sigmoidal configuration as seen *in situ* and in medial and lateral views, configurations as described for *Sigmoria s. lat.* Basal zone usually relatively long, around 1/3 of total acropodite length, inner surface directed anteriad, medial surface with or without broad, curved, laminate flange, latter forming convex inner surface. Anterior bend usually broad, poorly defined. Peak variable but usually relatively short and gently curved, apex near midlength, with or without variably narrow laminate flange on medial edge. Apical curve variable but usually broad, poorly defined. Distal zone of variable length and configuration, either broad and spatulate or with sides tapering smoothly and continuous-

ly, projecting downward from peak and coplanar with basal zone or not coplanar and extend-
ing laterad to various degrees, occasionally sharply curved into arch and lying beneath and
parallel to peak; with or without variably narrow medial flange and variable lateral flange, lat-
ter ranging from long and rectangular to narrowly triangular to small and gently rounded;
distal zone occasionally tilted mediad or laterad exposing medial or lateral flange in opposite
perspective. Termination simple, blunt to acuminate. Prostatic groove arising in pit on
prefemur, running along stem of acropodite and crossing from medial to lateral sides at
various locations, opening terminally on tip of distal zone.

Females agreeing closely with males in somatic features, except paranota more strongly
depressed, creating appearance of more highly arched body. Cyphopodal aperture broad, en-
circling 2nd legs, sides slightly elevated above metazonal surfaces. Cyphopods *in situ* located
lateral to 2nd legs, with corners of valves and receptacles visible in aperture. Receptacle small
to moderate, located on medial sides of valves, surface rugulose to finely granulate. Valves
small to moderate, subequal in size, directed caudolaterad, surfaces rugulose to finely
granulate. Operculum minute, hidden under free end of valves.

Distribution. — Piedmont Plateau of west-central North and South
Carolina between the Catawba and Broad rivers; and the southern Blue
Ridge Province of North Carolina, Tennessee, Georgia, and South Carolina
(Fig. 146). The range in the mountains extends onto the eastern and
southern escarpments, but forms have not been encountered in the Pied-
mont proper. There is no tangible northern boundary in the mountains.

Species. — Two, one in each of the above described regions. Other
workers may interpret the montane forms differently and recognize more
reproductive isolates, but I doubt if any different species await discovery.
Deltotaria thus resembles *Dynoria* in having two allopatric species, one in
the Blue Ridge Province and one in the Atlantic lowlands (see Shelley
1984b).

Deltotaria brimleii Causey

Diagnosis. — Color of paranota and metatergal stripes varying from red
to light orange, occasionally with sparkling, metallic sheen; coxal apophysis
in profile broadly triangular to slender with sides nearly parallel, moderate
to long, terminating at or beyond level of prefemoral process; acropodite
distally slender and fragile; medial flange located on peak or proximal part
of distal zone, with only slight lobe; lateral flange present, variable.

Ecology. — *Deltotaria brimleii* is a cove dwelling species.

Remarks. — *Deltotaria brimleii* occurs widely in the Southern Blue
Ridge Province (Fig. 146). Five names have been proposed for forms in this
area, but I think none are reproductively isolated. The only possible excep-
tion is the southernmost, occurring mainly in Georgia, for which the name
philia was proposed by Chamberlin (1949). Its acropodite is basically the
same as those of northern forms, and the narrow, indistinct lateral flange
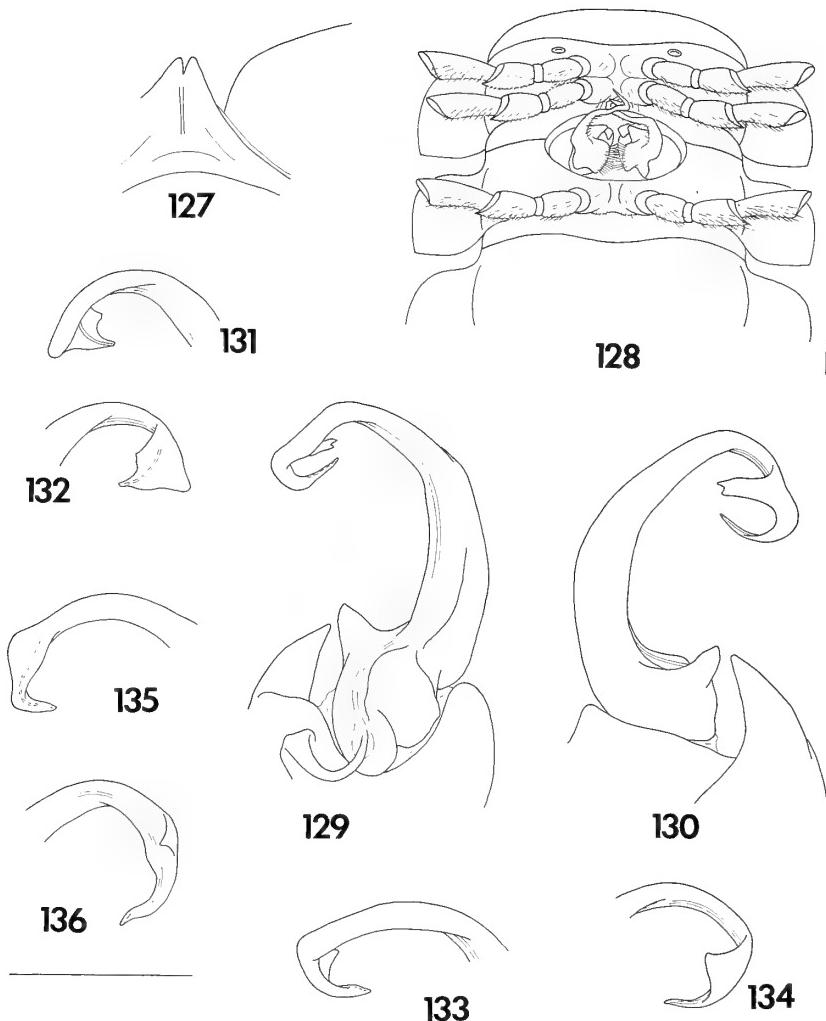
FIGS. 127-136. *Deltotaria brimleii brimleii*. 127, process of 4th sternum of holotype, caudal view. 128, gonopods *in situ,* ventral view of male from Montreat, Buncombe Co., NC. 129, left gonopod of the same, medial view. 130, the same, lateral view. 131, distal half of acropodite of male from Bent Creek Forest Experiment Station, Buncombe Co., medial view. 132, the same, lateral view. 133, distal half of acropodite of male from Gatlinburg, Sevier Co., TN, medial view. 134, the same, lateral view. 135, distal half of acropodite of male from 8 mi. NW Brevard, Transylvania Co., NC, medial view. 136, the same lateral view. Scale line for fig. 128 = 1.00 mm; line for other figs. = 1.00 mm for each.

continues the general north to south clinal trend toward smaller laminae. However, *philia* is distinguished by the form of the coxal apophysis, which in profile is narrow with nearly parallel sides and extends to or beyond the level of the distal zone, well beyond the level of the prefemur. With one exception, all the other material has broadly triangular apophyses that terminate at the level of the prefemoral process. In this exception, from Chimney's Picnic Area, GSNMP, Tennessee, the process is intermediate in both length and shape. Because of this sample and the absence of meaningful acropodal differences, I think *philia* is only a geographic race and therefore recognize two subspecies based on the length and configuration of the coxal process. Three names are placed in synonymy under the nominate subspecies.

Deltotaria brimleii brimleii Causey, new status   Figs. 127-136

Deltotaria brimleii Causey, 1942:165, Figs. 1-2. Chamberlin and Hoffman, 1958:30. Hoffman, 1961:25-28, Fig. 2c.
Deltotaria brimleardia Causey, 1950a:7-8, Figs. 2-3. Chamberlin and Hoffman, 1958:29.

Hoffman, 1961:30-31, Fig. 2b. **NEW SYNONYMY.**
Deltotaria tela Causey, 1950b:38-39, Figs. 3-5. Chamberlin and Hoffman, 1958:30. Hoffman, 1961:31-33, Figs. 1b, d, 2a. **NEW SYNONYMY.**
Deltotaria mariana Hoffman, 1961:28-30, Figs. 1a, e-h; 2d. **NEW SYNONYMY.**

Type specimen. — Male holotype (ANSP) collected by C.S. Brimley, 26 May 1923, at Swannanoa, Buncombe Co., NC. According to Hoffman (1961) there is a female topoparatype in the Causey collection, now at the FSCA. Hoffman presented a detailed description of the somatic aspects of the holotype, but as the genitalia are missing, he could only quote Causey's description (1942) and add a short interpretive comment. The following account of the pregonopodal sterna and the gonopods in "sigmoid" terminology is therefore prepared from a nearly topotypical male.

Diagnosis. — Coxal apophysis in profile moderately long and broadly triangular, extending to level of tip of prefemoral process, sides tapering rapidly to subacuminate tip; prefemoral process variable but usually present, occasionally vestigial.

Color in Life. — Paranota red; metaterga black with concolorous red stripes along caudal margins connecting paranotal markings; collum with red stripes along both anterior and posterior edges.

Male from Montreat, NC. — Fourth sterna with moderately long process between third legs, slightly shorter than widths of adjacent coxae (Fig. 127); segment 5 with minute paramedial knobs between 4th legs, much shorter than widths of adjacent coxae, and low rounded elevated areas between 5th legs; 6th sternum with slight recession along caudal edge to accommodate apical curvatures of acropodites.

Gonopodal aperture elliptical, 3.4 mm wide and 1.7 mm long at midpoint, indented slightly anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 128) with acropodites extending anteriolaterad from aperture and peaks overlapping in midline, curving slightly over opposite side and anterior margin with tips crossing. Gonopod structure as follows (Figs. 129-130): Coxal apophysis curving caudad at midlength, directed toward prefemoral process and terminating just below tip of latter, apically subacuminate. Prefemoral process short, wedge shaped. Acropodite moderately thick and heavy basally, becoming thinner and more fragile distad, arch high and gently curved, overhanging and extending just beyond level of prefemoral process; basal zone long, bowed caudad; anterior bend broad, poorly defined; peak high and gently rounded, apex at midlength; apical curve sharp, well defined; distal zone moderately long, projecting strongly laterad from peak, not coplanar with basal zone, curving sharply caudad at midlength and lying under and parallel to peak in medial view, sides tapering smoothly and continuously to acuminate tip, latter directed toward anterior bend. Medial flange clearly demarcated from peak, moderately long, arising at midlength (apex), curving gently outward to form narrow lobe, terminating at distal extremity of peak, margins smooth. Lateral flange with broad, rectangular, proximal lobe, equal in length to distal half of distal zone, with two sharp apical teeth, sides smooth, lobe terminating at midlength, flange then curving gently to terminus near tip of distal zone. Prostatic groove crossing to lateral side at apex of peak, continuing to terminal opening.

Female from Polk Co., NC. — Length 34.1 mm, maximum width 7.8 mm, W/L ratio 22.9%, depth/width ratio 62.8%. Cyphopods with receptacle moderate, surface rugulose. Valves moderate, equal, surfaces rugulose.

Variation. — This subspecies includes all forms with a moderate coxal process. The lateral flange is highly variable and may be relatively laminate with a curvilinear margin or be produced into variable lobes, which may be rectangular, broadly or sharply triangular, or spiniform. The longest or rectangular lobes obtain in the northern part of the range, in the form named *brimleii* by Causey (1942). In the southern form named *mariana* by Hoffman (1961), the distal zone is tilted mediad exposing part of the lateral flange in medial view (Fig. 135). As noted by Causey (1950b) in the description and later by Hoffman (1961), the form named *tela* vaguely resembles *Sigmoria (Sigiria) rubromarginata* because the margin of the lateral flange is slightly produced, and the distal zone projects more strongly laterad, exposing part of the medial flange in lateral view (Fig. 132). It occurs chiefly in the Pisgah National Forest in Buncombe County, North Carolina, and occasional males from other areas approximate this configuration, for example in Cocke County, Tennessee. I do not find the resemblance with *S. rubromarginata* very striking and consider it convergence; however, it might reflect an ancestral connection. Overall in *b. brimleii* there is a north to south clinal progression toward smaller, less distinct lateral flanges, which culminates in the inconspicuous lamella of the other subspecies. Differences also obtain in the arch of the acropodite and the curve of the distal zone, which is directed more strongly laterad in the western part of the range.

Distribution. — The southern Blue Ridge Province from the Linville River to the Little Tennessee Rivers in North Carolina and the northeastern corner of Georgia, and, east-west, from the escarpment in North Carolina to the Great Smoky Mountains of Tennessee (Fig. 146). Most of the material comes from south of the Black Mountains in North Carolina. The two northernmost records represent gonopodal fragments found with paratypes of *Sigmoria aberrans* and *S. conclusa,* both synonymns of *l. latior (Sigmoria),* in the Chamberlin collection. They possess the lateral flange and general acropodal configurations that occur in the northern part of the range (similar to the form in Figs. 129-130) and the localities therefore seem plausible. However, confirmation with fresh material is desirable. Specimens were examined as follows:

NORTH CAROLINA. — *Burke Co.,* Linnville Falls, M (segments 7-8), 12 August 1910, R.V. Chamberlin (RVC). *Mitchell Co.,* Altapass, M (segment 7 only), 11 August 1910, R.V. Chamberlin (RVC). *Buncombe Co.,* Montreat, M, 5 September 1977 (NCSM A1701); Swannanoa, M, 26 May 1923, C.S. Brimley (SNAP) TYPE LOCALITY; 5.2 mi. NW Avery Cr., along NC hwy. 191 at Blue Ridge Parkway nr. French Broad R., M, 1 June 1977, A.L. Braswell (NCSM A1595); Bent Creek Forest Experiment Station, M, F, 30 April 1939, N.B. Causey (ANSP); 8.8 mi. SE Asheville, Lake Powhatan, 2M, 5 September 1977 (NCSM A1706); and 11 mi. S Asheville, along co. rd. 3495, 0.3 mi. E jct. I-26, M, 3F, 16 June 1979 (NCSM A2769). *Polk Co.,* 1.5 mi. NNE Saluda, along co. rd. 1151, 0.3 mi. W jct. co. rd. 1142, M, F, 14 September 1977 (NCSM A1741). *Haywood Co.,* along US hwy. 276 S of Waynesville, M, 24 June 1961, H.V. Weems (FSCA); and 12 miles NW Waynesville, GSMNP, nr. Cataloochee School, 3M, 3F, 8 July 1976 (NCSM A916). *Swain Co.,* 2 mi. NE Bryson City, entrance to GSMNP nr. Deep Cr. Campground, M, F, 16 May 1978 (NCSM A1904). *Transylvania Co.,* 8 mi. NW Brevard, Pink Beds Rec. Area, M, F, 30 July 1958, R.L. and M.S. Hoffman (NMNH); 5 mi. NW Brevard, Sycamore Flats Rec. Area, M, 26 May 1958, L. Hubricht (RLH); between Rosman and Balsam Grove, M, 19 July 1961, R.L. Hoffman (RLH); and Toxaway Gorge SE Lake Toxaway, 3M, 16 July 1961, R.L. Hoffman (RLH). *Jackson Co.,* 4, mi. ESE Cullowhee, along Caney Fk. at John's Cr., M, 23 October 1970, F.A. Coyle (WAS). *Macon Co.,* 1.5 mi. SSE Highlands, Satulah Mtn., M, 4 June 1977, A.L. Braswell (NCSM A1592); Highlands, M, 1 July 1963, A. Douglas (RLH); and Coweeta Hydrologic Station, 2M, 6 July 1978 (NCSM A2318).
TENNESSEE. — *Cocke Co.,* GSMNP, Cosby Picnic Area, 3M, 8 August 1981 (NCSM A3716). *Sevier Co.,* Gatlinburg, along Ramsey Prong, M, 10 July 1947, H. Hansen (ANSP).
GEORGIA. — *Rabun Co.,* 12 mi ENE Clayton, along GA hwy 28 at W. Fork Chatooga R., M, F, 9 June 1978 (NCSM A2057).

Remarks. — The various forms of *b. brimleii,* which appear dissimilar because of differences in the curvature of the acropodite and the shape of the lateral flange, nevertheless connect through intermediate populations that bridge the gaps in the diagnostic characters of the nominal species reported by Hoffman (1961). In my view, none of the named forms demonstrates enough stability over a large enough area to be retained even at the subspecific level. For example, that previously known as *tela* (Figs.

131-132) has virtually a point distribution, being restricted to the Bent Creek Forest Area of the Pisgah National Forest in Buncombe County. The closest males to this site only vaguely resemble its types, and to retain this name for a single population is impractical.

In August 1981 I collected *b. brimleii* along the creek at Cosby Picnic Area, GSMNP, Tennessee, in precisely the same spots where I discovered *Sigmoria (Sigiria) rubromarginata* in May 1978. The latter was absent in 1981 as was the former on the previous trip. This appears to be a third ex-
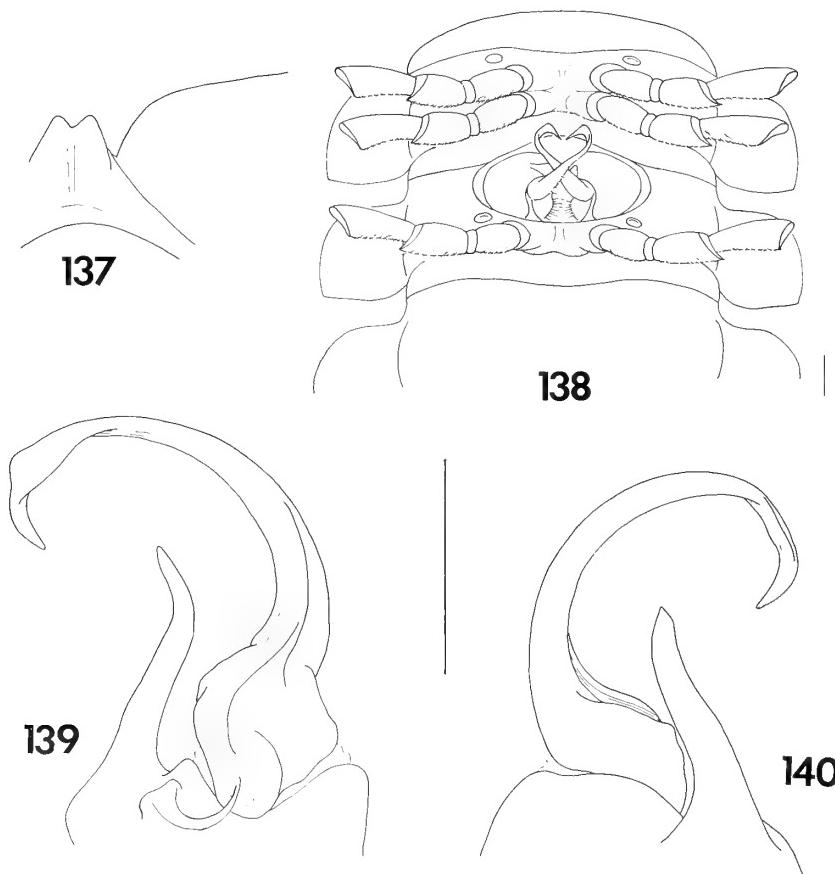
FIGS. 137-140.   *Deltotaria brimelii philia.*   137, process of 4th sternum of male from White Co., GA, caudal view.   138, gonopods *in situ,* ventral view of the same.   139, left gonopod of holotype, medial view.   140, the same, lateral view. Scale line for fig. 138 = 1.00 mm; line for other figs = 1.00 mm for each.

ample of two "sigmoid" species occurring at the same site but having their life histories adjusted so they are prevalent at different times of the year. For *Sigmoria (Cheiropus) australis* and *S. (C.) serrata* in Camden County, Georgia, I (1984a) suggested that this would minimize ecological competition if the species occupied similar niches. Future investigators should therefore determine whether both species occur at Cosby in June or July and whether there is a spring to summer decline in abundance of *S. (S.) rubromarginata* and a concomitant increase in *b. brimleii*.

Deltotaria brimleii philia (Chamberlin), new status   Figs. 137-140

Phanoria philia Chamberlin, 1949:101, Fig. 25.
Deltotaria philia: Chamberlin and Hoffman, 1958:30. Hoffman, 1961:34-35, Fig. 3b.

Type specimen. — Male holotype (RVC) collected by W. Ivie, 27 April 1943, at Clarksville, Habersham Co., GA.

Diagnosis. — Coxal apophysis in profile long and slender, extending to near or beyond level of tip of distal zone and well beyond level of prefemur, sides tapering gradually to subacuminate tip; prefemoral process absent or at most vestigial.

Color in Life. — Paranota red or orange, or red on outer margin fading into light orange on inner margin; metaterga black with concolorous stripes, red or orange or reddish on outside and orange on inside, along caudal margins connecting paranotal markings; collum with stripe along anterior margin.

Variation. — The males of *b. philia* agree closely with each other, and I detect no significant variation. Color, however, does vary. The specimens from Graham County, North Carolina, were uniformly orange, while those from the two Georgia locations were red. In South Carolina, the red on the outside of the paranota and stripes grades smoothly into light orange on the inside. These specimens also exhibit a sparkling, metallic sheen that is quite different from the glossy finish on other samples. The South Carolina locality is the most proximal to *lea,* which also displays this sheen, and the inner light orange hues may represent the influence of yellow pigmentation, which is the color found in *lea.*

Distribution. — Southern extremity of the Blue Ridge Province. The race occurs south and west of the nominate subspecies, and the Little Tennessee River appears to be a distributional boundary. Specimens were examined as follows:

NORTH CAROLINA. — *Graham Co.,* 9.5 mi. NNE Robbinsville, along Stecoah Cr. on co. rd. 1236, 0.5 mi. N jct. co. rd. 1235, 5M, 3F, 16 May 1978 (NCSM A1912).

SOUTH CAROLINA. — *Oconee Co.,* 15.5 mi. N Walhalla, Ellicott's Rock Wilderness Area Trail at Fish Hatchery off SC hwy. 107, Sumter Nat. For., M, F, 9 June 1978 (NCSM A2055).

GEORGIA. — *Habersham Co.,* Clarksville, M, 27 April 1943, W. Ivie (RVC) TYPE LOCALITY. *White Co.,* 7.2 mi. E Cleveland, along GA hwy. 255 at Chattahoochee R. and Habersham Co. line, 3M, F, 16 April 1978 (NCSM A1862). *Fannin Co.,* 11.2 mi. S Morganton, Deep Hole Campground off GA hwy. 60, Chattahoochee Nat. For., M, 9 July 1978 (NCSM A2348).
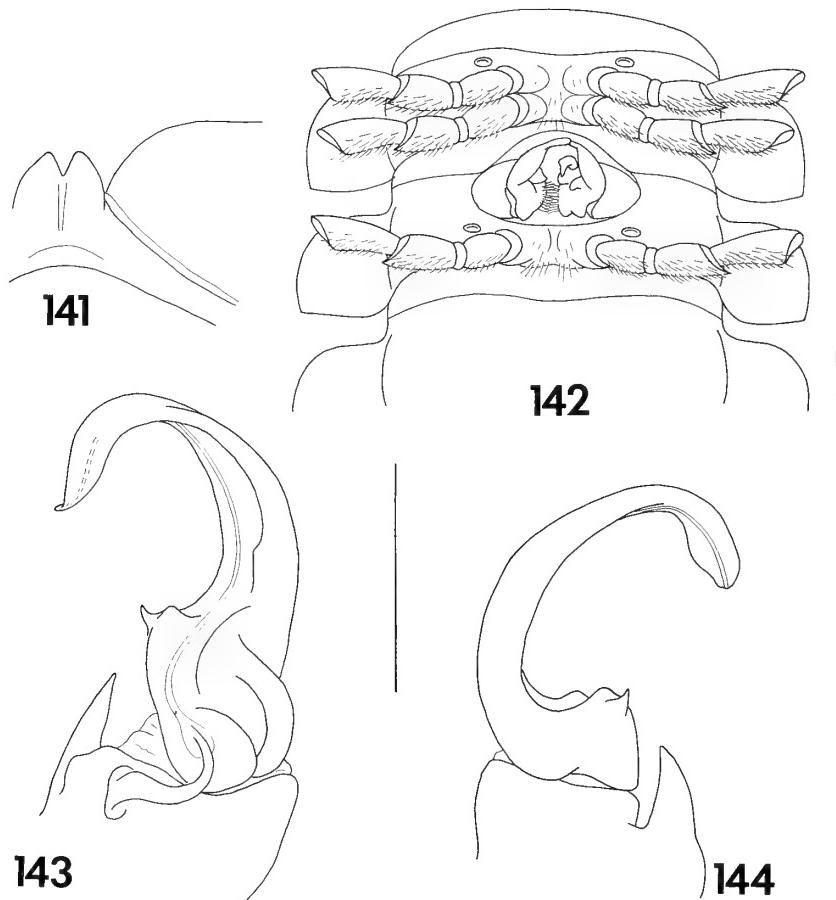
FIGS. 141-144.   *Deltotaria lea.*   141, process of 4th sternum of holotype, caudal view. 142, gonopods *in situ,* ventral view of male from Gaston Co., NC.   143, left gonopod of holotype, medial view.   144, the same, lateral view. Scale line for fig. 142 = 1.00 mm; line for other figs. = 1.00 mm for each.

Remarks. — Chamberlin (1949) and Hoffman (1961) reported that the acropodite of *b. philia* was apically hastate, but this appearance is actually caused by a profile view of the lateral flange.

Deltotaria brimleii intergrades

Males from the following locality possess coxal processess that extend beyond the level of the prefemoral process and are intermediate in length and shape between the two subspecies. The site is also somewhat intermediate, and I consider the specimens intergrades. Sample data are as follows:

TENNESSEE. — *Sevier Co.,* 7.3 mi. S Gatlinburg, GSMNP, Chimney's Picnic Area, 5M, F, 10 May 1978 (NCSM A1890).

Deltotaria lea Hoffman   Figs. 141-144

Deltotaria lea Hoffman, 1961:33-34, Figs. 1c, 3a. Filka and Shelley, 1980:29, Figs. 55-56.

This species was known only from the type locality when it was described and illustrated by Hoffman (1961). Filka and Shelley (1980) added supplemental notes on color, gonopodal variation, and reported a number of localities in North and South Carolina. No new material is available, but the pregonopodal sterna are characterized in more detail, and the gonopods are described in "sigmoid" terminology.

Type specimen. — Male holotype (NMNH) collected by L. Hubricht, 19 April 1956, 4.5 mi. SE Lincolnton, Lincoln Co., NC.

Diagnosis. — Color of paranota and metatergal stripes yellow, with sparkling metallic sheen; coxal apophysis in profile short and triangular, terminating below level of prefemoral process; acropodite distally broad and spatulate; medial flange extending nearly entire length of basal zone, greatly expanded and curved to form concave inner surface of this section; lateral flange absent.

Color in Life. — Paranota yellow; metaterga black with broad yellow stripes along caudal edges connecting paranotal markings; collum with stripe along anterior margin; colors with sparkling, metallic sheen.

Holotype. — Process of 4th sternum moderately long, slightly shorter than widths of adjacent coxae (Fig. 141); 5th sternum with low projections between anterior legs and flattened, elevated areas between 5th; 6th sternum convexly recessed along caudal margin to accommodate apical curvature of acropodites, 7th legs set slightly farther apart than 6th.

Gonopodal aperture ovoid, 3.8 mm wide and 1.4 mm long at midpoint, indented anteriolaterad, sides elevated above metazonal surface. Gonopods *in situ* (Fig. 142, not this specimen) with acropodites leaning mediad and apices overlapping in midline of aperture.

Gonopod structure as follows (Figs. 143-144): Coxal apophysis short, narrowly triangular, terminating below level of base of prefemoral process, sides tapering rapidly to acuminate tip. Prefemoral process short, uncinate, directed toward distal zone. Acropodite broad, medial and lateral surfaces expanded through peak (proximal 2/3 of length) into curved laminae, arch high and rounded, overhanging and extending beyond level of prefemoral process; basal zone moderately long and gently curved, inner surface concave; anterior bend broad, poorly defined; continuous through peak with apical curve; peak gently curved, apex at midlength; apical curve broad, poorly defined; distal zone flattened and spatulate, moderately long and directed downward from peak, coplanar with basal zone, flared outward apically; tip subacuminate. Medial flange a broad, curved lamina, located entirely on basal zone, arising proximally and terminating on distal extremity. Lateral flange absent. Prostatic groove crossing to lateral side at anterior bend, continuing to terminal opening.

   Female from Gaston Co., NC. — Length 34.2 mm, maximum width 8.8 mm, W/L ratio 25.7%, depth/width ratio 67.0%. Cyphopods with small receptacle, surface finely granulate. Valves small, equal, surfaces finely granulate.

Variation. — Filka and Shelley (1980) observed that gonopodal variation included the presence or absence of a minute prefemoral process, dimension of the tip of the distal zone, and diameter of the acropodal arch. In rechecking all individuals of *lea,* I find these features to vary randomly throughout the range. The prefemoral process is present on only four individuals: the holotype and one each from Cleveland County, North Carolina, and York and Cherokee counties, South Carolina. Similarly, occasional random males have longer distal zones that extend farther from the peak. All, however, have short coxal processes that terminate below the level of the prefemur and broad medial flanges that extend nearly the entire length of the basal zone.

I also checked for facial setae in males of *lea.* All lack epicranial and interantennal series, about half have frontal setae (1-1), and nearly all have genal setae, usually one per side but occasionally 2-2 or 3-3. Three individuals have a short row of three marginal genal setae continuing from the merged clypeal and labral series.

Ecology. — *Deltotaria lea* occurs in predominantly deciduous woodlands under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — An area about 70 miles long in the Piedmont Plateau of the Carolinas between the Catawba and Broad Rivers, being particularly abundant in the Kings Mountain region on the border of the two states. Localities are detailed in Filka and Shelley (1980).

Remarks. — In addition to color and gonopodal differences, *lea* is also a larger, more robust species than its congener. The paranota project more directly laterad in *lea,* interrupting the slope of the dorsum and imparting a somewhat flattened appearance. In contrast, *brimleii* is more vaulted, and the paranota are more continuous with the slope of the dorsum, extending sharply downward toward the substrate.

Because of its peripheral occurrence in the state, Filka and Shelley (1980) recommended that *lea* be assigned to the Of Special Concern conservation status in North Carolina.

PART III. ECOLOGY
By Rowland M. Shelley

HABITATS. — The characteristics of the cove environments inhabited by species of *Sigmoria s. lat.* were detailed by Shelley (1981a). Theses sites also are preferred by *ainsliei, aphelorioides,* and *prolata (Falloria),* the *haerens* group *(Cheiropus),* the subgenus *Dixioria* (wherever the habitat occurs in the more widely spaced mountains north of the Nolichucky River), and *Deltotaria brimleii.* I have collected the nominate subspecies of *trimaculata (Rudiloria)* in New York and West Virginia, both times in places with cove features. However, it remains to be seen how applicable this habitat is to the subgenus *Rudiloria* as a whole. From what Hoffman (pers. comm.) related about the site where he discovered *whiteheadi (Sigiria),* it also appears to be a cove species and, along with *truncata (Sigiria),* one of only two that can occur in rhododendron litter.

In the piedmont and Atlantic lowlands, *Deltotaria lea,* the subgenus *Cleptoria,* and *persica* of the *planca* group *(Cheiropus)* are found mostly in predominantly hardwood areas under thin layers of leaves on relatively firm substrates near water. This environment also is preferred by the subgenus *Croatania,* although these forms frequently are encountered in predominantly or exclusively pine woods. Farther south and east, *australis, planca,* and *serrata (Cheiropus)* occur in a variety of predominantly hardwood sites, which include the best spots available in the generally unfavorable coastal environments.

West of the Appalachian Mountains, the forms in the Cumberland Plateau and Nashville Basin Provinces of Tennessee occur in a variety of biotopes. Cove environments are widespread in the former, especially north of highway I-40, but surprisingly they are shunned by *picapa (Falloria).* My assistants and I searched in vain for around 40 man-hours in coves near Wartburg, Frozen Head State Park, and other areas in central Morgan County before finally encountering one male and one female in oak woods near the type locality. These were in a different microhabitat, under deep piles of leaves well removed from water. Clearly, *picapa* has ecological preferences different from those of cove dwelling congeners. However, *forficata (Falloria),* occurring north and south of *picapa,* does occur in coves, and the same is true for *abbreviata (Falloria).* Farther south, *houstoni (Falloria)* prefers dry, open areas but still seeks shelter under thin layers of

leaves on relatively firm substrates. Cove habitat becomes steadily rarer westward into central Tennessee, and the species of the *mimetica* group *(Falloria)* therefore opt for the best hardwood sites available, with the more secluded and moist ones being preferred. Certain areas of central Tennessee resemble those in piedmont Georgia and South Carolina, and the millipeds likewise are found in the same kind of microhabitats along banks of streams or in moist spots. Exceptional individuals occasionally are encountered in xeric environments, as in Cedars of Lebanon State Park, Wilson County.

SYNTOPY. — I (1981a) previously reported that only one species of *Sigmoria s. lat.* occurs at a given site, and until recently I had not encountered any syntopic apheloriine species, even among different genera. The first instance was the discovery of *australis* and *serrata (Cheiropus)* together in Camden County, Georgia (Shelley 1984a), wherein *australis* was reported as an undescribed species of *Hubroria*. These two species apparently avoid competition by being dominant at different times of the year. The same may be true for *australis* and *Dynoria medialis* Chamberlin at Kolomoki Mounds State Park, Early County, Georgia. A third example may involve *rubromarginata (Sigiria)* and *Deltotaria brimleii* at Cosby Picnic Area, GSMNP, Tennessee. I collected the former there in May 1978 and the latter in exactly the same spots in August 1981, so visits in June and July may yield both. Another example of syntopy came to my attention in July 1984, when Dr. Hoffman sent a male of *whiteheadi (Sigiria)* and one of *l. latior (Sigmoria)* which were taken within a few feet of each other at the type locality of the former. Because *latior* is a ubiquitous species not restricted to cove environments, it does not occupy the same niche as *whiteheadi*. There still are no clear examples of syntopy between cove dwelling congeners, which is in accordance with Gause's theorem that two species cannot indefinitely coexist if they have identical ecological requirements. However, a possible example of syntopy among cove species involves *coronata* and *brooksi (Dixioria)* in Johnson County, Tennessee. More precise knowledge of the habitats of these species is needed before this can be confirmed.

Fig. 145.   Distribution of *Sigmoria*. Known discontinuities in the southern half of the main part of the range are shown, but a smooth curve is drawn around the range extremes north of the isthmus in southwestern Virginia. Discontinuities may exist in West Virginia, Ohio, Pennsylvania, and other northern areas, but insufficient sampling has taken place to detect them. The ranges of the groups in the Cumberland Plateau and Nashville Basin of Tennessee, while not known to abut or overlap, are very close and hence are drawn as a single unit. From east to west, the disjunct southern areas correspond to *planca* and populations of *australis,* with one Alabama population of *rileyi* occurring on the northern periphery of the central one. The dot in north-central Alabama corresponds to the Jefferson County record of *rileyi*.

145
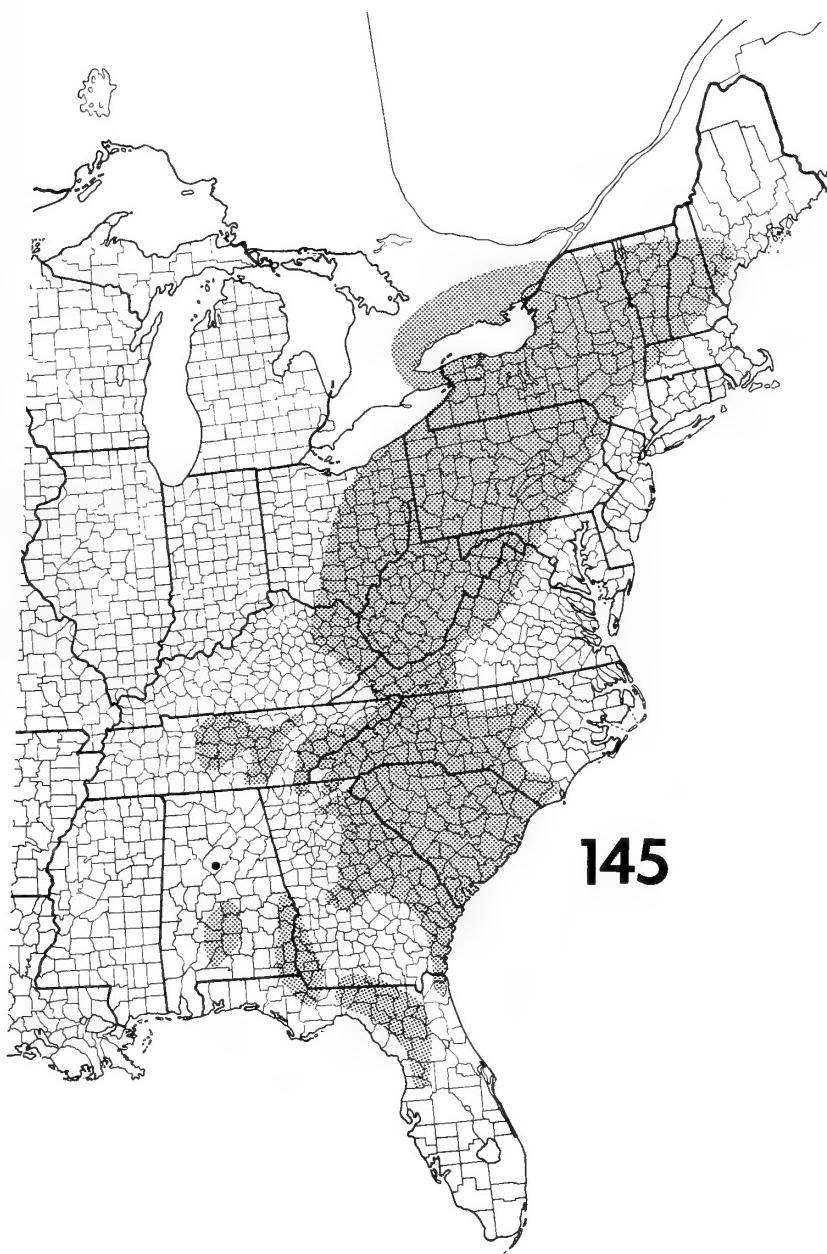
PART IV.   DISTRIBUTION
By Rowland M. Shelley

DISTRIBUTION OF SIGMORIA. — With the inclusion of the new speices and those in the synonymized genera, the distribution of *Sigmoria s. lat.* is enlarged to encompass the shaded areas in figure 145. Overall, the genus ranges from northern New England and southern Ontario to northern peninsular Florida, and from the Atlantic Ocean in South Carolina and Georgia as far west as central Tennessee and central Alabama. A smooth curve is drawn around range extremes in the north, where sampling has been sparse, but known discontinuities are shown from southwestern Virginia southward, where the greatest species diversity occurs and where sampling has been more intensive. The two areas are divided by an isthmus in southwestern Virginia, the northern area being occupied by *Rudiloria* and by one species each of *Dixioria* and *Sigmoria s. str.*, and the southern by the rest of the genus. Physiographically, the main part of the generic range spans the St. Lawrence, Connecticut, Hudson, Delaware, Potomac, Ohio, New, Cape Fear, Yadkin, Catawba, Savannah, Altamaha, and St. Marys Rivers, taking in parts of the New England, Adirondack, Ridge and Valley, Blue Ridge, Piedmont Plateau, and Coastal Plain Provinces.

In central Tennessee, an apparently disjunct area in the Nashville Basin and Cumberland Plateau is occupied by members of the *mimetica, picapa,* and *translineata* groups *(Falloria)*. This area is separated from the main one by the Tennessee River and probably represents a real distributional gap. Repeated searches for *Sigmoria* in the northern half of the hiatus in Anderson, Morgan, and Roane counties yielded only *Brachoria*. Farther south, the Tennessee River Valley in Rhea, Meigs, and Bradley counties has been chiefly cleared for pasture or other agricultural uses, and not even *Brachoria* is found there now.

Obvious disjunctions also occur in the extreme south, involving members of the subgenera *Cheiropus* and *Cleptoria*. The most notable gap is the apparent absence of *Sigmoria s. lat.* from most of the southern half of Georgia. Both *australis (Cheiropus)* and *rileyi (Cleptoria)* occur in three disjunct populations, two of which are mostly or completely in Alabama (Figure 68). *Sigmoria (Cheiropus) planca* is the southernmost species and the only one in this area wholly detached from the main generic range.

DISTRIBUTIONS OF SPECIES AND SPECIES GROUPS. — Figure 125 depicts the distributions of *ainsliei, aphelorioides,* and *prolata (Falloria),* and figure 147 shows occurrences within the GSMNP. *Sigmoria aphelorioides* occurs south of the GSMNP and the Little Tennessee River, whereas *ainsliei* is in the Park and the adjacent Ridge and Valley Province. Of the ten "sigmoid" species known from the Park, *rubromarginata*

(Sigiria) is the dominant form in the northern section, north and east of US highway 441. *Deltotaria brimleii* also is abundant, and both species occur as far south as Gatlinburg and the Deep Creek area, on the west and east sides, respectively. South and west of this highway the fauna is dominated by members of the subgenus *Falloria*.

The distributions of species of *Falloria* in the Tennessee disjunct area are shown in figure 126. The *picapa* and *translineata* groups are restricted to the Cumberland Plateau, whereas the *mimetica* group is concentrated in the Nashville Basin but spreads onto the Highland Rim on either side. The sample of *mimetica* from Cheatham County is the westernmost of the genus *Sigmoria*.

The fauna in the lowlands east and south of the Blue Ridge Province is so complex that, for clarity of presentation, it must be shown on two maps (for distributions of the *haerens* and *planca* groups, see Shelley 1982, 1984a). Figure 68 depicts locality records for *australis* and the subgenus *Cleptoria*, and figure 49 shows records for *Croatania*.
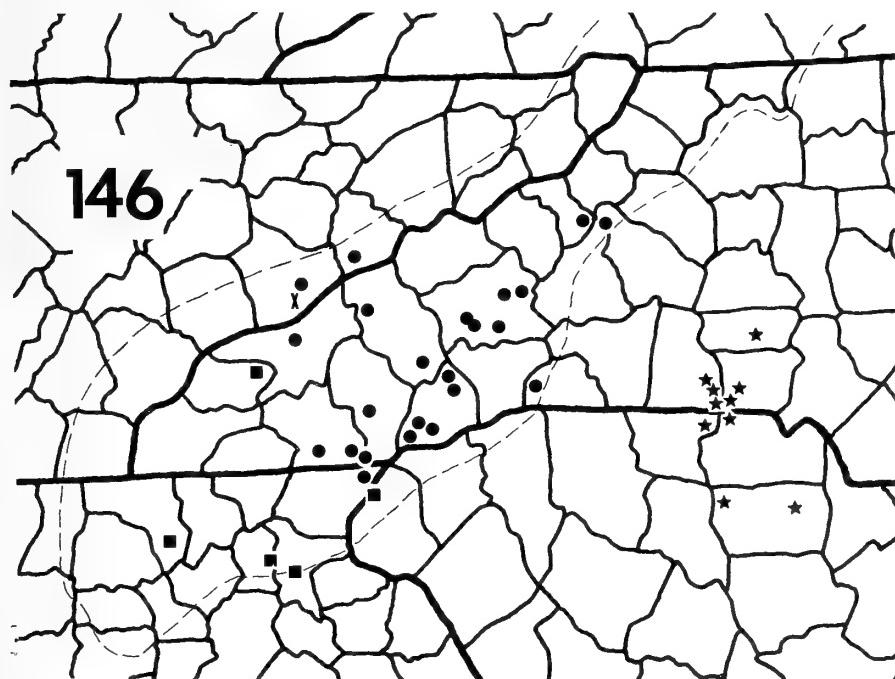
Fig. 146. Distribution of *Deltotaria*. Dots, *b. brimleii;* squares, *b. philia;* X, *brimleii* intergrades; stars, *lea.* The dashed line denotes the approximate boundary of the Blue Ridge Province.

Sigmoria (Cheiropus) australis and *rileyi (Cleptoria)* occur in three disjunct areas. The westernmost sample of *rileyi*, from the southern extremity of the Cumberland Plateau, is some 40 miles north of the closest record of *australis*, in the Fall Zone. *Sigmoria rileyi* also occupies the northern periphery of the Chattahoochee segregate of *australis*. This river bisects the latter area and does not form a distributional limit as it does for *Dynoria medialis* (see Shelley 1984b). The eastern segregate of *australis* hugs the Atlantic Ocean in South Carolina and Georgia, spanning the Savannah, Ogeechee, Altamaha, and Satilla Rivers. It is unknown south of the St. Marys River, but as its distribution in coastal Georgia is similar to that of *serrata*, *australis* may also occur in northeastern Florida.

Most of the records shown for the subgenus *Cleptoria* in figure 68 are along the Savannah River, where field efforts were concentrated. Although *rileyi* undoubtedly is more widespread, it probably does not occur much farther west because the area around Atlanta has been sampled reasonably thoroughly. In central Georgia the ranges of *rileyi*, *persica (Cheiropus)*, and *Dynoria medialis* are almost exclusive (see Shelley 1984a, b), suggesting that they occupy similar niches. The actual distribution of *bipraesidens* may parallel that of the South Carolina species, *robusta*, in ranging nearly to the Blue Ridge Front. *Sigmoria (Cleptoria) abbotti* hugs the southern side of the Savannah River in both the Piedmont Plateau and the Coastal Plain, but the South Carolina species are limited to the Piedmont south of the Enoree River. The distributions of *shelfordi* and *arcuata* are as stated previously (Shelley 1980a, 1981b), except the Oconee County male is reassigned to the former. *Sigmoria macra* occurs in a band north of these species, and *robusta* occupies a somewhat triangular area in the western tip of South Carolina.

An updated distributional map for the subgenus *Croatania* (Figure 49) includes localities listed in Shelley (1977) and new ones cited herein. The most significant additions are those for *simplex*, formerly known only from the type locality. This site is near the northern range limit, and the species actually extends well past the Fall Zone into the central Coastal Plain. New records for *saluda* extend its range eastward through the Fall Zone to the inner edge of the Coastal Plain. Range additions to *catawba* are minor and areas where it was expected from previous records. *Sigmoria (Croatania) yemassee*, still known only from the two original collections in Jasper and Beaufort counties, and *australis (Cheiropus)* are the only two "sigmoid" species in the southern tip of South Carolina, where even *latior* is absent.

The subgenus *Dixioria* (Figure 45) occupies a small area around the contiguous corners of North Carolina, Tennessee, and Virginia, from Tazewell County in Virginia southward to the Nolichucky River. It is known only

from the Blue Ridge Province in North Carolina and Tennessee, but in Virginia *coronata* spreads northward into the Ridge and Valley Province. *Sigmoria (Dixioria) coronata, pela, watauga,* and *wrighti* have sharp distributional limits, but only a few records are available for *acuminata* and *brooksi.* Further exploration may expand their boundaries in Tennessee and Virginia; *dactylifera,* however, is restricted to central Ashe County, North Carolina.

Aside from the subgenus *Dixioria,* comparatively little is known about the forms of *Sigmoria s. lat.* occurring north of North Carolina. Vast areas remain to be investigated in West Virginia, Kentucky, Ohio, and Pennsylvania. Available records, plotted in figure 17, reveal clustering of *l. latior (Sigmoria)* and *t. kleinpeteri (Rudiloria)* in southwestern Virginia, the only region to have received much attention. Father north, the plotted ranges of *guyandotta, rigida,* and *mohicana (Rudiloria)* are subject to future expansion; however, the scattered records of *t. trimaculata (Rudiloria)* probably outline its area fairly accurately. The absence of the genus from piedmont Virginia is curious, and the recent discovery of *whiteheadi (Sigiria)* along the escarpment in Patrick County may indicate more surprises in lowlands to the east. Explorations of this area are left to future investigators, and clues to potentially productive environments are available in the ecological accounts here and in Shelley (1977; 1980a; 1981a, b, c; 1984b).
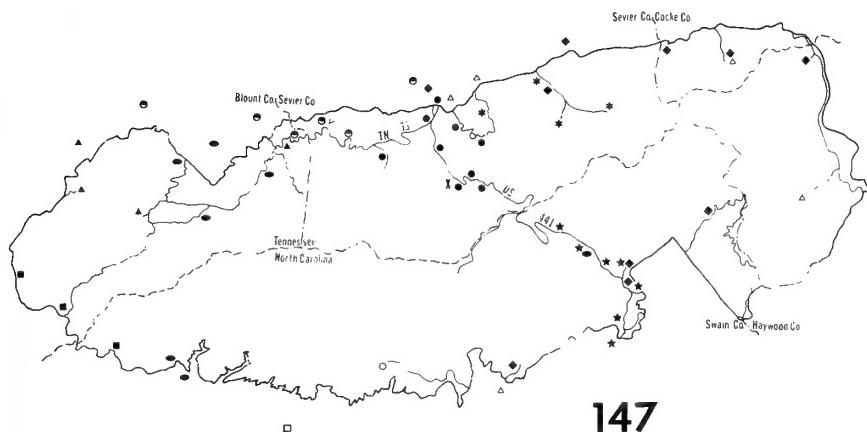
FIG. 147. Distributions of species of *Deltotaria* and *Sigmoria* in the Great Smoky Mountains National Park and vicinity. Diamonds, *rubromarginata;* stars, *tuberosa;* circle, *nantahalae;* ovals, *translineata;* squares, *lyrea;* solid triangles, *fumimontis;* half-shaded dots, *ainsliei;* dots, *bidens;* asterisks, *prolata;* open triangles, *D. b. brimleii;* open squares, *D. b. philia;* X, *D. brimleii* intergrades.

TABLE 4. Distribution of Species of *Sigmoria* by Physiographic Provinces

+ Occurrence within the province.
E Endemic to the province.

Taxon	No. (Table 3, Figs. 151-152)	New England Adirondack	Coastal Plain	Piedmont Plateau	Blue Ridge	Ridge & Valley	Appalachian Plateaus	Interior Low Plateaus
trimaculata	1-3	+				+	+	
guyandotta	4						E	
mohicana	5						E	
rigida	6						E	
pela	7				E			
acuminata	8				E			
coronata	9				+	+		
watauga	10				E			
wrighti	11				E			
brooksi	12				E			
dactylifera	13				E			
latior	14-17		+	+	+	+	+	
stenoloba	18			E				
quadrata	19			E				
laticurvosa	20			E				
catawba	21			E				
saluda	22			E				
simplex	23		+	+				
yemassee	24		E					
rileyi	25			+			+	
abbotti	26			E				
bipraesidens	27			E				

Species	No.			
robusta	28		E	
arcuata	29		E	
shelfordi	30		E	
macra	31		E	
australis	32	E		
stibarophalla	33	E		
divergens	34	E		
haerens	35	E		
divaricata	36	E		
thrinax	37			E
agrestis	38		+	+
serrata	39			E
planca	40			E
persica	41		E	
rubromarginata	42	E		
austrimontis	43	+	+	
whiteheadi	44	E		
triangulata	45	E		
nigrimontis	46-49	E		
inornata	50	E		
truncata	51	E		
sigirioides	52	E		
areolata	53	E		
stenogon	54	E		
disjuncta	55	+	+	

TABLE 4. Distribution of Species of *Sigmoria* by Physiographic Provinces (Continued)

+ Occurrence within the province.
E Endemic to the province.

Taxon / No. (Table 3, Figs. 151-152)	New England Adirondack	Coastal Plain	Piedmont Plateau	Blue Ridge	Ridge & Valley	Appalachian Plateaus	Interior Low Plateaus
nantahalae 56				E			
leucostriata 57				E			
xerophylla 58				+	+		
aphelorioides 59				E			
translineata 60				E			
fumimontis 61				E			
lyrea 62				+	+		
ainsliei 63				E			
bidens 64				E			
prolata 65				E			
tuberosa 66				E			
forficata 67						E	
houstoni 68						E	
abbreviata 69						E	
picapa 70						E	
mimetica 71							E
pendulata 72							E
crassicurvosa 73							E
Number of Species	1	7	18	35	5	10	3
Percent of Genus	1.5%	10.8%	27.7%	53.8%	7.7%	15.4%	4.6%
Number of Endemic Species	—	4	12	29	—	7	3
Percent of Genus	—	6.2%	18.5%	44.6%	—	10.8%	4.6%

Mostly widely distributed species: *latior* (5 provinces); *trimaculata* (3 provinces).

PHYSIOGRAPHIC PROVINCES AND ENDEMISM. — Table 4 lists the species of *Sigmoria s. lat.* by physiographic province (Hunt 1967), including also the extent of endemism. Immediately apparent is the preponderance of total taxa and endemics in the Blue Ridge Province, in both cases more than those of the two adjacent regions combined. Slightly over half the total species are represented at least partly in the Blue Ridge, and well over 1/3 of the endemics occur there. The Piedmont and Appalachian Plateaus rank second and third in both categories, and there are no endemics in the Ridge and Valley Province. All three species in the Interior Low Plateaus of central Tennessee are endemic. The southeastern Coastal Plain has four endemics, which are of interest in view of the flat topography and generally unfavorable habitats. Although *disjuncta (Sigiria)* is listed from two provinces, it occurs along the base of the escarpment in South Carolina and Georgia and does not really span the Blue Ridge and Piedmont Plateau regions. In contrast, *simplex (Croatania)* clearly spans the Fall Zone boundary between the Piedmont Plateau and Coastal Plain in South Carolina, inhabiting sizeable portions of both regions. Table 4 also shows the great adaptability of *latior (Sigmoria),* which occurs in five provinces of vastly different environments; the large distribution of *trimaculata (Rudiloria)* does not cover nearly as great a range of biotopes.

DISTRIBUTION OF DELTOTARIA. — The distributions of the species of *Deltotaria* are shown in figure 146. The strict correlation of *brimleii* with the boundaries of the Blue Ridge is clearly evident, although southern populations occur along the edge of the escarpment in Georgia in a manner similar to *S. (Sigiria) disjuncta.* Approximately 55 miles separate the two allopatric species, both of which are sympatric with several species of *Sigmoria s. lat.*

PART IV.   COLORS AND COLOR PATTERNS
By Rowland M. Shelley and Donald R. Whitehead

One intriguing aspect of *Sigmoria s. lat.* is the complex variation in color and color pattern. The first observation a collector makes is the color of his specimens, and Table 1 lists the diversity of hues and arrangements. Colors and color patterns tend to be ignored in xystodesmid systematics, but we find their geographic patterns extremely informative.

COLOR PATTERNS. — The three general color patterns cluster geographically as shown in figure 148. The northern 2/3 of the range is mostly comprised of the middorsal spot pattern, which overlaps that of the uniformly black metaterga (paranotal spots only) in southwestern Virginia.

148

||||| midddorsal metatergal spots

• ||||| uniformly black metaterga

||||| metatergal stripes
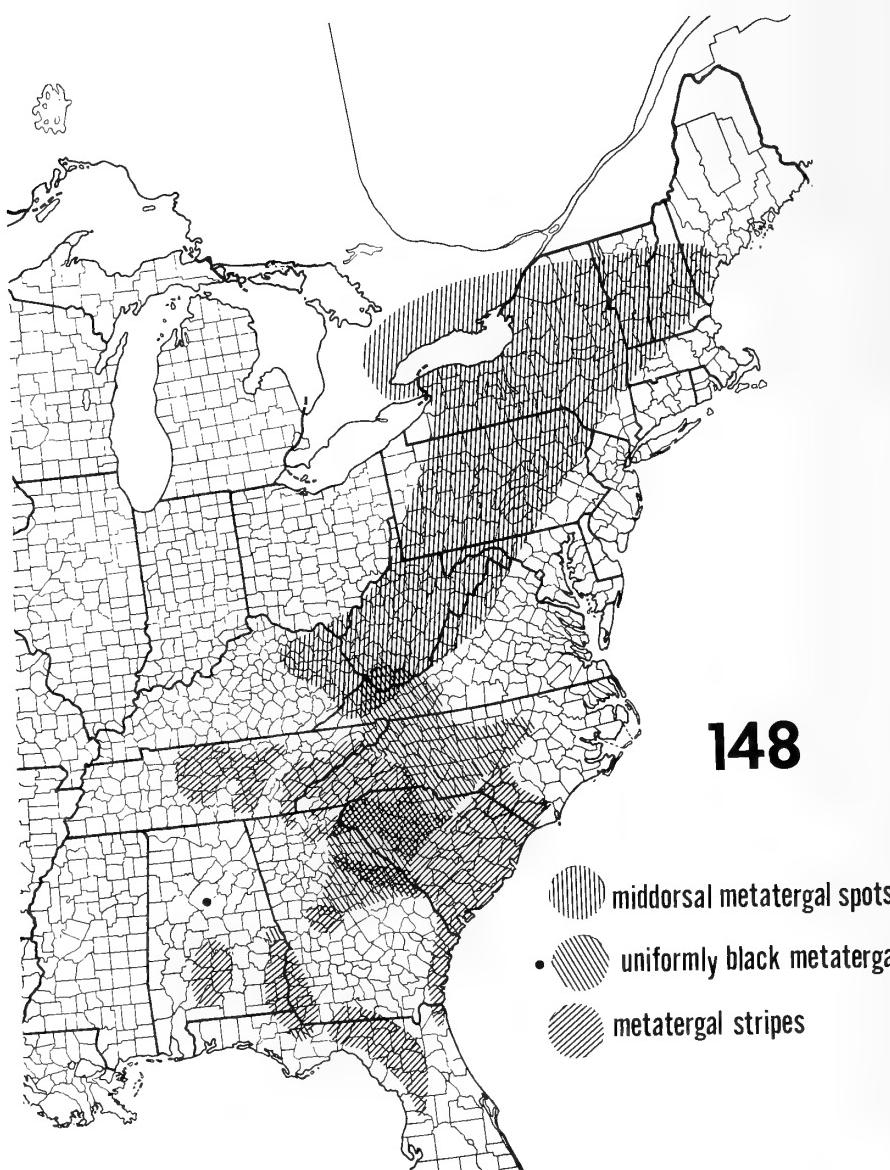
Fɪɢ. 148.   Approximate distributions of the color patterns of *Sigmoria*.

The latter pattern extends broadly into North Carolina, narrows into South Carolina where it overlaps forms with metatergal stripes, then widens across the Savannah River into piedmont Georgia, where it overlaps a finger of the red stripe pattern and abuts on an isolated population of the latter. The metatergal stripe pattern, occurring in Tennessee and throughout the southern section of the Blue Ridge Province, extends southeastward into South Carolina where it overlaps forms with uniformly black metaterga. The distribution of the striped pattern widens in the Coastal Plain, extending northward back into North Carolina and southward to the southern extremity of the main generic range. Except for the area in northern Alabama and the northern and southern extremities of that bisected by the Chattahoochee River, the striped pattern is also the one found in the southern disjuncts. The peripheral discontinuities in the Chattahoochee segregate represent the southernmost samples of *australis (Cheiropus)* and the Lee County population of *rileyi (Cleptoria)* in the north, both with uniformly black metaterga. The "unstriped" pattern in northern Alabama also reflects *rileyi,* and additional field work is needed to determine the size of the Jefferson County area.

Striped forms omitted from this map include some variants of *t. trimaculata (Rudiloria)* from West Virginia; *whiteheadi (Sigiria)* from Patrick County, Virginia, at the eastern periphery of the uniformly black metatergal pattern; and *mohicana* and *rigida (Rudiloria),* which probably are striped as judged from original descriptions and faded preserved material. Other omissions result from the lack of clear information about the patterns. *Sigmoria (Cleptoria) bipraesidens,* a member of an otherwise unstriped subgenus, is said to be striped (Hoffman 1967) and occurs at the range periphery of the unstriped taxa, but this needs confirmation. The color pattern of *yemassee (Croatania)* is not known, but this coastal species occurs in an area occupied by known striped species and probably also displays this pattern.

With the exceptions noted above, color pattern distribution in *Sigmoria s. lat.* can be generalized as follows: the metatergal spot pattern takes up much of the northern 2/3 of the range, and the uniformly black metaterga and metatergal stripe patterns share rather equally the southern 1/3, the area with the greatest species diversity. In the latter, the unstriped pattern tends to occur in the northern and central parts, and the striped pattern more to the west, east, and south. Sympatry between the latter two patterns is in a relatively broad band, and elsewhere the patterns tend to abut with geographically proximal borders.

COLORS. — The metatergal stripe pattern can be subdivided by colors (Figures 149, 150). As with the general color patterns described above, the

colors of the stripes tend to cluster and are not randomly dispersed. For example, blue stripes (Figure 149) tend to occur to the west of red stripes, predominating in central and southeastern Tennessee. Red stripes are found over a much larger area including the southern disjuncts. *Sigmoria (Cheiropus) planca,* the southernmost species, is omitted from figure 149 because its stripes are more orange than red (Shelley 1984a). However, it does bridge the wide red/red hiatus along the Georgia/Florida boundary. Two species of *Falloria* tend to have white or whitish stripes (Figure 150): the northern one, *leucostriata,* has concolorous paranotal spots, whereas the southern one, *nantahalae,* has red paranotal markings. In the central Smokies, the red, white, and blue stripe patterns overlap, the red

149

🔴 red stripes

🔵 blue stripes
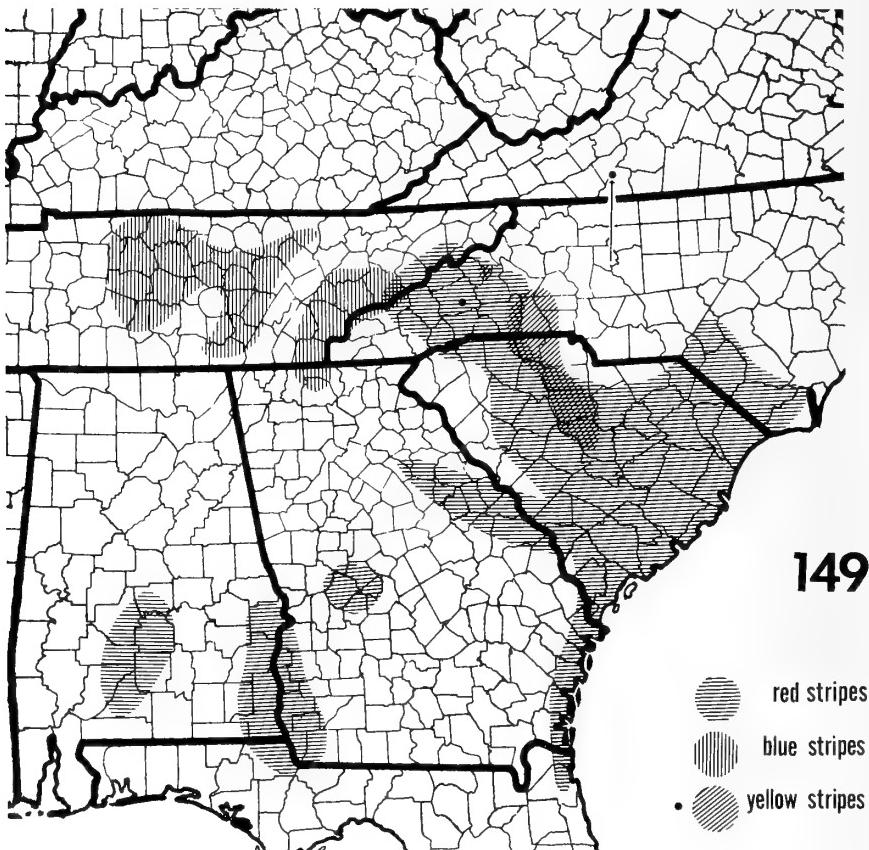
· 🟡 yellow stripes

FIG. 149.   Approximate distributions of the red, blue, and yellow metatergal stripe colors in *Sigmoria.* The dots in Buncombe County, North Carolina, and Patrick County, Virginia, show isolated locations of yellow stripes in *areolata* and *whiteheadi,* respectively.

represented by *rubromarginata (Sigiria)* and the other two colors by species of the subgenus *Falloria*.

South and east of *nantahalae, disjuncta* and *stenogon (Sigiria)* tend to have concolorous violet or purple paranotal spots and metatergal stripes. The separated distribution shown in figure 150 is somewhat misleading, because intervening populations of *divergens (Cheiropus)* also tend to be dark.

Yellow stripes occur mainly in a band in the Carolinas partly occupied also by red stripes. Small pockets of yellow stripes represented by forms of *Sigiria* are isolated elsewhere in the red stripe area *(areolata, inornata)* and in the uniformly black metatergal area in Virginia *(whiteheadi)*. *Sigmoria (Sigiria) areolata* and *whiteheadi* are known from point distributions and are not known to be polymorphic for color, but *inornata* is polymorphic and may display red, orange, or yellow stripes throughout its range.

IMPORTANCE OF COLOR AND COLOR PATTERN. — Among the eastern Xystodesmidae, most genera of the Rhysodesmini and all genera of the Apheloriini have bold colors on a black background, whereas none of the Nannariini or Pachydesmini display striking contrasts. Some boldly patterned forms apparently are mimetic, as judged from the occurrence of similar colors among sympatric taxa representing distinct lineages. For in-
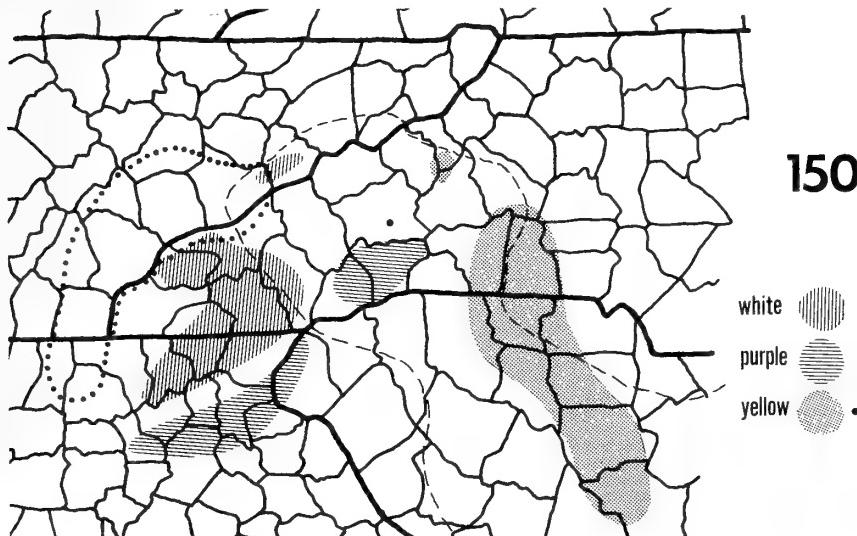
FIG. 150. Approximate distributions of the white, yellow, and violet/purple metatergal stripe colors in *Sigmoria*. The dotted and dashed lines denote boundaries of the blue and red stripes, respectively. The dot in Buncombe County indicates the location of the yellow striped *areolata*.

stance, blue stripes appear in the same geographic areas in both *Brachoria* and *Sigmoria s. lat.*, whereas forms of *Brachoria* in the range of the subgenus *Dixioria* display the yellow paranota/black metaterga of the latter. In other instances, sympatric taxa differ in colors; for example, the red striped *Deltotaria brimleii* overlaps various blue striped species of *Falloria* in the southern Blue Ridge Province. Farther north, however, it is broadly sympatric with the red striped *rubromarginata (Sigiria)*.

Geographic distributions of the various colors and patterns considered together with probable instances of convergence suggest informative transformation series useful for phyletic analysis. This information is probably as valuable and as easy to interpret as gonopod structure, and thus equally important in developing a system of relationships within *Sigmoria s. lat.* The combination of color and geography is also useful in field identifications once distributions are well mapped. Some species have distinctive patterns within their areas of distribution, so previously unassignable females may be identifiable if colors and provenance are known. Table 3 facilitates such determinations.

PART VI. RELATIONSHIPS WITHIN SIGMORIA
By Donald R. Whitehead and Rowland M. Shelley

In this part, we outline analytical problems encountered in the study, discuss details of the subgenera of *Sigmoria,* resolve subgeneric relationships, and close with a discussion of "mosaic" evolution. We use the term "mosaic" only for observed geographic patterns found in apparently natural groups of primarily allopatric and parapatric species-group taxa which seem to lack cladistic congruence in their various character states. This kind of pattern in millipeds and in other groups of comparatively non-vagile animals resembles a jigsaw puzzle.

Some other terms and notations deserve explanation. Color pattern is usually denoted by a fraction, wherein "red/red" means red paranotal spots and red metatergal stripes, and "yellow/black" indicates yellow paranotal spots and no metatergal stripes. The term "eastern" refers to eastern North America, from the seaboard to the central Great Plains, including the Ozarks. Relationships are depicted by equations; for example, *"Croatania = simplex + (yemassee + (catawba + saluda))"* means that within the subgenus *Croatania, simplex* is sister to the other three species, and *yemassee* is sister to *catawba* plus *saluda*. These cladistic statements, which are exactly analogous to mobiles, are given instead of pictorial trees. Use them with associated maps to visualize implied vicariance patterns.

ANALYTICAL PROBLEMS. — With few exceptions, species diagnostic characters used in *Sigmoria s. lat.* are exclusively in gonopodal structures, and it is difficult to construct satisfactory transformation series. These are complex structures, yet some types of complexities may arise from comparatively simple alterations. Hence, apparently major gonopodal differences may be evidence for nothing more than species level differences. The main somatic features used herein are the relative length of the process of sternum 4 and color patterns. There is no reason to assume convergence in either gonopods or in sternum 4 if derived states of these characters occur in geographically coherent patterns of proximal taxa. We assume the reverse, that geographic coherence represents shared ancestral features. Color patterns must be viewed more critically, not only because of infraspecific variation, but also because we find evidence of mimetic convergence both within *Sigmoria s. lat.* and among related genera. Hence, color patterns also tend to be geographically coherent, but they less convincingly indicate common ancestry.

The genus *Sigmoria* is a cohesive geographic entity (Figure 145) having properties resembling those of a single, rapidly differentiating or fragmenting species. This implies that the history of *Sigmoria* is quite brief, perhaps post-Pleistocene. We infer a continuous, widespread, geographically varied ancestor in rather recent times, which colonized habitats as they became available and subsequently fragmented. Such fragmentation is easy to envision, since most species now occupy specialized cove habitats. Where the allopatric/parapatric mosaic pattern is retained, distributional shifts must reflect ancestral proximity patterns, with range expansion by one segregate achieved only by displacement of another. Present day distribution patterns directly reflect vicariance.

We use the term "incomplete synapomorphy" for a peculiar form of homoplasy occurring in the "mosaic", when the same plesiomorphous and apomorphous states of a character are shared by both members of a sister pair and, by inference, their common ancestor. If characters in the ancestor varied along different geographic gradients, then fragmentation must have cut across character gradients in such a way that derived states of some characters were shared by parts of two or more segregates. Given low vagility in these organisms, there is no reason to assume that the derived character states diffused among the segregates before further fragmentation occurred. These geographically coherent but noncongruent apomorphous character states ("incomplete synapomorphies") suggest common ancestries, but they do not define lineages in diagnostic terms.

Consider what happens when a pepperoni pizza is sliced into wedges, with the pepperoni representing apomorphies. Some pieces of pepperoni will be

divided between two adjacent wedges, some slices will have contiguous boundaries, and still other slices will share a point of contact. In *Sigmoria,* the subgenera represent the pie wedges and character state distributions represent the pepperoni. Radial slicing is represented by contact in the southern Blue Ridge by proximal, relatively plesiomorphous members of *Cheiropus, Sigmoria, Sigiria,* and *Falloria.* As the *Sigmoria* pie was sliced by nature, the simplest type of slicing is the most probable. Thus, the first slices should have been cut across the pie rather than in a wedge by wedge sequence.

Ideally, a cladistic hypothesis based solely on morphological character states should be developed for *Sigmoria,* similar to the generic and tribal hypotheses given in chapter VIII. However, the numerous species, combined with apparent convergences, clines, and instances where variation crosses cladistic lines, create a geographic mosaic of reproductive isolates in which the taxonomic or geographic distributions of many character states lack congruence. Our initial attempts at cladistic analyses, which were made without considering geographic distributions, met with failure. We here describe a solution for this mosaic problem, which should apply also to similar problems in other organisms. We consider a character-based cladistic analysis premature at this time. Future investigations should focus on development of other character systems.

Our approach to analysis is based on the observation that the genus seems to have some properties of a single species. We simply test as a null hypothesis the premise that the pieces of the mosaic interlock in a pattern consistent with the properties of a biological species. Hence, the species and subspecies are treated as pieces of a largely two dimensional jigsaw puzzle. Their geographic fit is conspicuous in most instances, thus allowing a search for geographic and character congruence. We did detailed mapping of the species and subspecies taxa, searched for both continuities and major discontinuities in the characters of geographically proximal taxa, and identified as major components (i.e., subgenera) those clusters of taxa that are most strongly discontinuous from proximal taxa.

With one notable exception, *Sigiria,* we are satisfied that our eight allopatric/parapatric subgenera are monophyletic. Remaining is the problem of finding the one (out of 135, 135 possible dichotomous combinations) cladistic arrangement for the subgenera that best fits known facts of geographic and character distributions. The solution, again, is based on a combination of geographic and cladistic inference.

In terms of vicariance partitioning, the subgenera are distributed in a pattern resembling an irregularly cut, eight slice pizza pie. Most slices are adjacent to at least two others, and residual commonality exists in the boundary

areas. The pie is sliced but virtually intact — there is little obvious extinction pattern except for gaps between conspecific populations. The slicing pattern itself may be obvious but incomplete. As in the pizza, this might not be noticed until one attempts to isolate the slice.

Maps, figures, and tables both in this paper and in previous papers by Shelley form the basis for character analysis. Out-groups to determine polarity of character states are iterative, and hence polarities may differ among different groups and at different levels.

THE SUBGENERA. — Each subgenus differs in structural diversity, diagnosis, and geography. Thus, some have single species groups, whereas others are more speciose. Some have satisfactory autapomorphies, while others are linked by transformation series or are grouped only by linkage patterns or by "incomplete synapomorphies" which do not apply to all included taxa. Most have only allopatric/parapatric taxa, but others have disjunct and/or sympatric taxa. Except perhaps for *Sigiria*, we think that each subgenus is monophyletic, regardless of its internal composition and despite the lack of complete independence with respect to all structural features. Those features termed "incomplete synapomorphies" at the generic level, here are the opposite; they are plesiomorphies within the subgenus.

We discuss each subgenus in turn, based on a preliminary cladistic hypothesis (Figure 154): genus *Sigmoria* = subgenera *((Rudiloria + Dixioria) + (Sigmoria + (Croatania + Cleptoria))) + Cheiropus + (Sigiria + Falloria)*. Undesirable features of this hypothesis are summarized and resolved in our review of subgeneric relationships. Figure 156 is the revised cladistic hypothesis.

Rudiloria. — This subgenus includes only the *trimaculata* group, with five allopatric specific and subspecific taxa *(t. trimaculata,* #1; *t. kleinpeteri,* #2; *trimaculata* intergrades, #3; *guyandotta,* #4; *mohicana,* #5; *rigida,* #6)* as mapped in Figure 151, areas 1-6. Detailed distributions are not yet available, and the species and subspecies hypotheses may not survive. The subgenus might even prove to be monotypic. This is the northernmost subgenus, grouped with the partly sympatric, more southern *Dixioria* by apomorphous gonopod orientation. Although divergent in details of gonopodal structure, notably the enlarged prefemoral processes and accessory teeth in *Dixioria,* these two subgenera share other features perhaps indicative of common ancestry.

Aside from sharper acropodal bends in *rigida,* there is resemblance between it and *pela (Dixioria)* (compare Figures 15 and 20), although the range of *ridiga* is separated from that of *Dixioria* by more divergent forms of *Rudiloria.* Both species have acropodites of about the same thickness, and both have a similarly shaped tooth at about the same distance from the

tip of the distal zone. We consider this a shared ancestral condition between *Rudiloria* and *Dixioria*. Various features of *rigida* (metatergal stripes; prefemoral process present; acropodite short, not looped, without flanges, with tooth), but not the short process of sternum 4, represent a probable ground plan for *Rudiloria*. The thin, fragile acropodites of various forms of
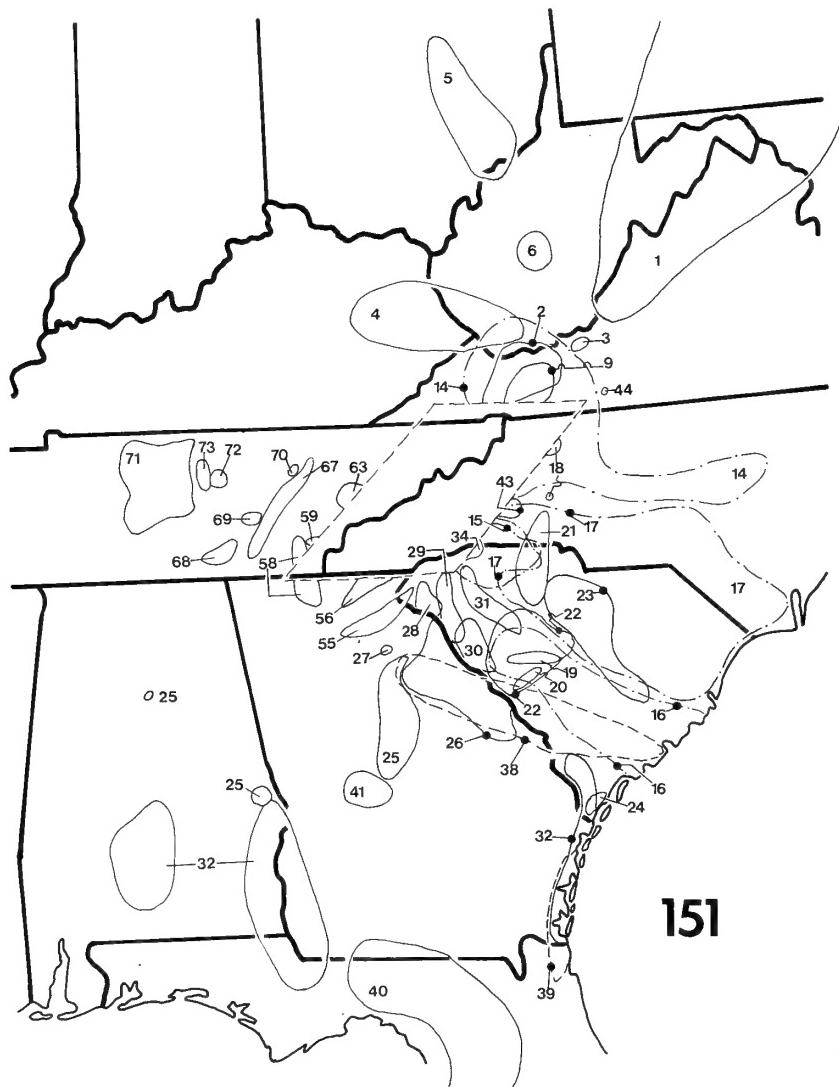
FIG. 151.   Generalized species distributions in *Sigmoria;* numbers as in Table 3.

TABLE 5.   Apomorphous character states in *Rudiloria*

Character	Taxon						
	1,WV	1	2	3	4	5	6
Acropodite looped	x	x	x	x	—	—	—
lobed	—	—	x	—	x	—	—
bent	—	—	—	—	—	x	xx
not toothed	x	x	x	x	x	x	—
Prefemoral process absent	—	—	—	—	x	x	—
Process of sternum 4 short	—	—	—	—	x	x	x
Metatergal spots (not stripes)	—	x	x	x	x	—	—

Taxa numbered as in Table 3: WV indicates West Virginia samples. Character states range from plesiomorphous (−) to most apomorphous (xx).

Rudiloria and *Dixioria* are perhaps convergent in this respect with those of such taxa as *sigirioides* (which is geographically proximal to *pela*), *stenogon,* and *triangulata (Sigiria).*

Some characteristics of members of *Rudiloria* are summarized in table 5. Presence of dorsal metatergal spots rather than stripes in *guyandotta, t. kleinpeteri, trimaculata* intergrades, and all but a few western *t. trimaculata* is unique within the genus. This color pattern may reflect relationship with *Dixioria* in which neither dorsal spots nor stripes are present. However, since the two subgenera are partly sympatric, the color pattern might represent mimetic convergence. The process of sternum 4 is moderately long in both subspecies of *trimaculata,* an ancestral condition shared with most members of *Dixioria.* These two subspecies also differ from other *Rudiloria,* as well as from *Dixioria,* in having a strongly looped acropodite, a derived state. Two species, *guyandotta* and *mohicana,* lack a prefemoral process, another derived state.

In the nominate subspecies of *trimaculata* the looped acropodite tapers smoothly and continuously to the tip, whereas *t. kleinpeteri* has expansions or lobes at the lowest point in the loop or midlength of the distal zone. In West Virginia, adjacent to the latter's range, is *guyandotta,* in which the distal zone is expanded and extends a short distance below the peak. The lamella is smaller than the lobes of *t. kleinpeteri* but has the same general contours, and *guyandotta* may be merely a form of the latter with the distal zone shortened and the lobes reduced. However, the transition is sudden, with no intermediate forms such as occur between the two subspecies of *trimaculata,* and *guyandotta* also lacks the prefemoral process found in *trimaculata.* In Ohio, *mohicana* has nearly the same acropodal configura-

tion as *guyandotta* but with slightly sharper angles and without the distal zone expansion. In West Virginia, *rigida* has basically the same acropodite as *mohicana* but with still sharper bends, and it also has a tooth and a prefemoral process.

Thus, there is a circular gradient from a looped acropodite without lobes or expansions (and with a prefemoral process), to one with flanges, to a shorter, non-looped one with flanges (and without a prefemoral process), to a short one with slight angles and without flanges, to a short one with strong angles (and with a tooth and a prefemoral process). Between *t. trimaculata* and *t. kleinpeteri* the character change is bridged by intermediates, whereas between *t. kleinpeteri* and *guyandotta* it is abrupt. More collecting is needed in Kentucky, West Virginia, and Ohio to determine the nature of other transitions. The acropodal configuration in *mohicana* could connect directly with that in *t. trimaculata,* and the possibility of a clinal continuum is enhanced by the fact that West Virginia samples of *t. trimaculata* agree with *mohicana* in having metatergal stripes rather than dorsal spots. Just as the acropodite of *guyandotta* may be shortened from that of *t. kleinpeteri,* the structure in *mohicana* may be a reduction of that of *t. trimaculata.*

The looped acropodites of *trimaculata* are convergent with those of *ainsliei* and *aphelorioides (Falloria),* approximately 125 miles to the south, and with *Apheloria,* whose range overlaps all three species. Other aspects of the acropodites of these forms do not exhibit such similarities.

Dixioria. — This subgenus includes only the *pela* group, with seven closely spaced species taxa as mapped in figures 151-152, areas 7-13. These taxa share a distinctive body form, and they share with *Rudiloria* a distinctive gonopod orientation.

The distribution of *Dixioria* overlaps that of *Rudiloria,* is adjacent to that of *Sigiria,* is overlaid by that of the ecological generalist *latior (Sigmoria),* and is separated by a small gap (ca. 45 miles) from that of *Croatania. Dixioria* and *Rudiloria* share with *Sigmoria s. str., Croatania,* and *Cleptoria* some non-gonopodal features, including the tendencies to lack metatergal stripes and to have relatively long processes on sternum 4. Furthermore, the enlarged prefemoral processes of *Dixioria* and the more southern *Croatania* occur in close geographic proximity. An alternative relationship *(Rudiloria, Dixioria, Sigmoria s. str., Sigiria, and Falloria)* is suggested by geographic proximity of forms having relatively delicate acropodites. However, as we show later in this chapter, we now regard *Dixioria* and *Rudiloria* as a lineage sister to the rest of the genus.

The most differentiated member of the *pela* group is *dactylifera* (#13), which has the process of sternum 4 short (a derived state) and lacks an accessory tooth (polarity undetermined). If lack of an accessory tooth is

ancestral, *dactylifera* is sister to the rest of the *pela* group. Otherwise, it might be a derived element.

In *Dixioria* the species are mostly parapatric with abrupt transitions, a prime reason for considering them reproductively isolated along with the apparent syntopy between *brooksi* (#12) and *coronata* (#9) in Tennessee. More sampling is needed in the transition areas between the forms in this state and Virginia to determine if changes occur as abruptly as in the heavily sampled areas in North Carolina.

A trend towards a longer tooth and a longer distal zone from *coronata* (#9) to *wrighti* (#10) occurs in steps involving the geographically intermediate *watauga* (#11), which has an apomorphous, more distal accessory tooth. Thus, a clinal continuity in one respect is matched by a discontinuity in another, and recognition of *watauga* as a separate species is the most conservative action consistent with the present knowledge. *Dixioria* may actually contain as few as three species, and we treat it as a superspecies in which a detailed cladistic hypothesis is unwarranted.

Sigmoria. — This subgenus (Figures 151-152, areas 14-20) includes the *quadrata* group with two adjacent piedmont species (*quadrata*, #19, and *laticurvosa*, #20) and the *latior* group with two ecologically differentiated species (the widespread, polytypic *latior*, #14-17, and the bipopulational *stenoloba*, #18). The two groups are associated by the flange on the peak of
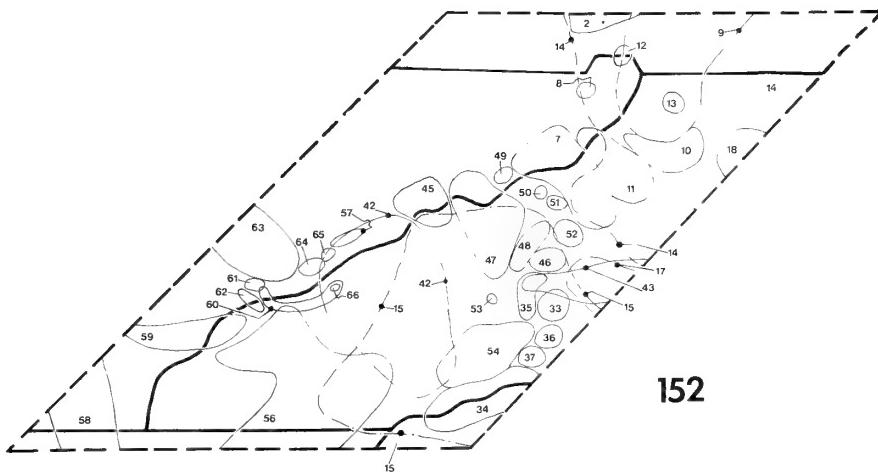
FIG. 152. Generalized distributions of *Sigmoria* species in the southern Blue Ridge Province; numbers as in Table 3.

the acropodite and by geography: *Sigmoria = (latior + stenoloba) + (quadrata + laticurvosa).*

A clear and convincing pattern of geographic races and intergrades is evident in *latior*, far more so than elsewhere in the genus wherein fragmentation patterns are more complete. With its broad ecological tolerances, *latior* is able to spread between localities and is found moving on the substrate more often than any congener. The ecologically generalist nature of *latior* may represent an ancestral feature, if the ancestor of the genus was widespread and geographically varied.

Sigmoria (Sigmoria) latior overlays the ranges of numerous other taxa. Its distribution clarifies the relationship between the *quadrata* and *latior* groups, which otherwise would be disjunctive. It also helps explain the curious, disrupted range of *stenoloba*, which lacks metatergal stripes. If this condition were viewed as synapomorphous, the only possible ancestor for *stenoloba* would be *l. latior*; thus, a species would be derived from a sympatric subspecies. However, lack of metatergal stripes in *l. latior* and *stenoloba* is shared with various members of *Rudiloria, Dixioria, Croatania,* and *Cleptoria.* Also, the gonopodal flanges of *latior (s. lat.)* are more developed than those of *stenoloba*, an apomorphic condition arguing against shared ancestry between *l. latior* and *stenoloba*. Hence, we accept a sister relationship between *latior (s. lat.)* and *stenoloba*, with the disrupted range of the latter resulting from displacement by the more successful *latior* (Shelley 1981a). *Sigmoria (Sigmoria) stenoloba* is known from Wilkes and Catawba counties, North Carolina, its two allopatric populations separated by about 40 miles and distinguished only by minor gonopodal differences.

Certain taxa of *Sigiria* (notably, *whiteheadi, areolata,* and some individuals of *inornata*) have yellow paranotal spots and yellow metatergal stripes as occur in some populations of *l. munda (Sigmoria),* but they otherwise most closely resemble various red/red forms of *Sigiria.* We consider yellow/yellow as an "incomplete synapomorphy", given a probable transformation series of red/red to yellow/yellow to yellow/black, because red/red and yellow/yellow occur in both *Sigmoria s. lat.* and *Sigiria.* Mimetic convergence is unlikely. For example, *whiteheadi* structurally fits best with *austrimontis (Sigiria)* but is syntopic with yellow/black *l. latior.* It seems to share a distant common ancestry with *latior (s. lat.)* but to have retained an intermediate, ancestral yellow/yellow coloration. It might seem to represent a range extrusion from *austrimontis* which failed to achieve the *l. latior* color pattern, but a range extrusion is incompatible both with a simple fragmentation pattern and with the major range disjunction between *austrimontis* and *whiteheadi.* The disjunctive *whiteheadi* represents a remnant of an ancestral yellow/yellow continuum.

Both members of the *quadrata* group occur within the range of *saluda (Croatania).* This is one of rather few examples of secondary sympatry among ecologically restricted species. Both species of the *quadrata* group have metatergal stripes, and we infer that their ancestry was to the southeast of the range of the ancestral component which lacked stripes. The more widespread *saluda* is thus the incursive element. If the ancestry of the *quadrata* group was to the southeast of that of *Croatania,* then the subgenus *Sigmoria* itself was ancestrally eastern.

The subgenus *Sigmoria* is characterized by the reflexed acropodite tip, a feature also found in some samples of *arcuata,* which we think is a sister element within *Cleptoria* and which therefore might represent ancestral conditions found in *Cleptoria* and *Croatania.* However, a reflexed tip also is found in *stenogon (Sigiria)* and *fumimontis* and *aphelorioides (Falloria).*

Aside from the lack of metatergal stripes in some members of the *latior* group as well as in various species of *Cleptoria* and *Croatania,* a relatively long process of sternum 4 occurs in the latter two subgenera and in the *quadrata* group. Both conditions are "incomplete synapomorphies", homoplasious with respect to one another and to various gonopodal features yet geographically coherent.

Sigmoria (s. str.) is a discrete component of *Sigmoria (s. lat.),* but it is less clear how it relates to other subgenera. It appears to be a geographic subdivision with residual connections to other proximal subgenera along what are now disconnected clinal gradients. Geographic considerations and a general similarity of gonopods with those of *arcuata (Cleptoria)* seem to suggest a relationship of *Sigmoria s. str.* with *Croatania* and *Cleptoria* (see figure 154). In turn these subgenera might seem related to *Rudiloria* and *Dixioria* because of the presence in some members of a relatively long process on sternum 4 or the absence of metatergal stripes. However, there also are gonopodal similarities between species of *Sigmoria s. str.* and certain species of *Sigiria* and *Cheiropus* (notably *areolata* and *stibarophalla,* previously assigned to the *latior* group by Shelley 1981a). For reasons developed later in the chapter, we now consider *Sigmoria s. str.* to share common ancestry with *Sigiria* and *Falloria* (see Figure 156).

Croatania. — This subgenus contains only the *catawba* group, with four species taxa (Figure 151, areas 21-24). *Croatania* has an autapomorphy, the irregularly notched expansion of the basal zone. Possibly also autapomorphous, though shared with the more northern *Dixioria,* is the large prefemoral process. The spine on the basal zone in some but not all *Cleptoria* is considered homologous with the enlarged basal projection on the notched expansion of *Croatania.* This, in combination with the generally robust gonopods of both subgenera, specifies sister relationship. "In-

complete synapomorphies" in color and the form of the process of sternum 4 seem to link *Croatania* and *Cleptoria* with *Sigmoria, Dixioria,* and *Rudiloria,* but we provide a more satisfactory set of subgeneric relationships later in the chapter.

Relationships within *Croatania* are clear. In *simplex* (#23), the process of sternum 4 is apomorphous in being short rather than long, and in *catawba* (#21), *saluda* (#22), and *yemassee* (#24) the prefemoral process is apomorphous in being more greatly enlarged. This represents an obvious east/west vicariance. Over 100 miles downstream in the Savannah River Valley, *yemassee* differs from the other taxa in having smaller teeth in the expansion and a decidedly more proximal medial flange, which occurs on the distal extremity of the basal zone. This represents a second, south/north vicariance. In summary, *Croatania = simplex + (yemassee + (catawba + saluda))*.

This simplicity is confused by the geographic distribution of color patterns. The northernmost taxon, *catawba,* is yellow/black, as are proximal populations of *simplex.* Farther south, approaching the range of primarily red/black *Cleptoria, saluda* and central populations of *simplex* also are red/black. Farther east, populations of *simplex* in the Fall Zone and Coastal Plain are red/red, and we predict that *yemassee* also is red/red as are all coastal congeners. Color patterns are not uniformly distributed by taxa, but they do form geographically coherent distributions. In some instances, they might be explained by mimetic convergence, but this explanation should apply only to sympatric taxa, not to such parapatric taxa as the geographically proximal species of *Cleptoria* and *Croatania.* Herein lies the basis for interpreting the color combination yellow/black or red/black as an "incomplete synapomorphy": its geographic distribution links various allopatric but geographically proximal taxa of these subgenera with *Sigmoria* and *Dixioria.* Where a similar color combination is found elsewhere, as in the southernmost population of *australis (Cheiropus),* it evidently is disconnected and may be a random convergence.

Shelley (1977) proposed dispersal hypotheses to account for distributions of species of *Croatania,* but they are inappropriate because the animals are not sufficiently vagile. Although the species inhabit a greater diversity of biotopes than those of the proximal or sympatric *rileyi (Cleptoria)* and *quadrata (Sigmoria)* groups, their habitat requirements are still too narrow to allow them to spread through an area with so many biotopes.

Cleptoria. — This subgenus contains only the *rileyi* group (Figure 151: *rileyi,* 25; *abbotti,* 26; *bipraesidens,* 27; *robusta,* 28; *arcuata,* 29; *shelfordi,* 30; *macra,* 31). Various differently distributed "incomplete synapomorphies", including a "bird's head" acropodite and/or presence of a basal

spine, confirm monophyly. The basal spine is homologous to the enlarged basal projection on the notched expansion in proximal taxa of *Croatania,* hence these subgenera are sister groups. Puzzles within the *rileyi* group include the resemblance of *arcuata* in some gonopodal features to *Sigmoria s. str.,* the complex distributions and variations of *macra* and *shelfordi,* and the disjunctive populations of *rileyi* and *shelfordi.*

Sigmoria (Cleptoria) arcuata is sister to the rest of the group, having a relatively slender acropodite, a laminate rather than thickened lateral flange, no distal lobe ("bird's head"), and, in the southernmost population (in Abbeville County, South Carolina), a reflexed tip (see table 6). Whether these conditions are ancestral or secondary is unclear, but they suggest features found in *Sigmoria s. str.* and perhaps represent other instances of "incomplete synapomorphy". Presence of the basal spine confirms placement of *arcuata* in *Cleptoria.* There is obvious circular reasoning in the postulate that gonopods are ancestrally stocky in *Croatania/Cleptoria,* if the relatively slender gonopods of *arcuata* are used to suggest a still more distant common ancestry with *Sigmoria.* Once again, "incomplete synapomorphy" provides a geographically plausible explanation.

A curious puzzle is the isolated western, apparently relictual population of *shelfordi,* which is separated from the main range of the species by *arcuata* and which lies adjacent to the range of *robusta.* This form lacks the prefemoral process, perhaps an ancestral "incomplete synapomorphy" shared with *arcuata.* We believe that the absence of a prefemoral process in *rileyi* and *bipraesidens* represents convergence with *arcuata* and the western form of *shelfordi,* because of the disrupted geographic distribution of this character state. Proximal populations of *shelfordi* and *macra* resemble one another, and although there are no clear intergrades, the taxa may even be conspecific. The proximal populations, the easternmost of *shelfordi* and southernmost of *macra,* tend to have a spur on the peak of the acropodite, and the former also tends to lack the basal spine as does *macra* throughout its range. Thus, although there is no synapomorphy for *shelfordi* and *macra,* the "incomplete synapomorphies" link them as sister species. Together, they are sister to the remaining four species, which are grouped by an upward shift of the medial flange from the basal zone toward the peak. The presence of the isolated western population of *shelfordi* is accordingly explained by vicariance partitioning: *arcuata* separated first; *shelfordi* + *macra* separated next, in an arcuate band to the south of *arcuata;* then, the range of *shelfordi* became subdivided. Next, *robusta* became isolated, as the "bird's head" became more sinuate in the southern taxa. Later, the medial flange shifted still farther onto the peak and the prefemoral processes were lost in *rileyi* and *bipraesidens.* Thus, the cladistic

TABLE 6. Apomorphous character states in *Cleptoria*

Character	Taxon									
	25	27	26	28	31n	31s	30e	30w	30W	29
Acropodite massive	XX	XX	XX	XX	XX	XX	X	X	X	—
thickened, not laminate	XX	XX	XX	XX	XX	XX	X	X	X	—
"bird's head"	XXX	XXX	XXX	XX	XX	XX	X	X	X	—
medial flange on peak	XX	XX	X	X	—	—	—	—	—	—
with spur on peak	—	—	—	—	—	X	X	—	—	—
without basal spine	—	X	—	—	X	X	X	—	—	—
Prefemoral process absent	X	X	—	—	—	—	—	—	X	X
Without metatergal stripes	—	X	—	—	—	—	—	—	—	—

Taxa numbered as in Table 3, with letters to indicate north, south, east, or west populations; W represents the isolated population of *shelfordi*. Character states range from plesiomorphous (−) to most apomorphous (xxx).

hypothesis: *Cleptoria* = *arcuata* + ((*shelfordi* + *macra*) + (*robusta* + (*abbotti* + (*rileyi* + *bipraesidens*)))).

Except for *bipraesidens,* the color pattern of *Cleptoria* is red/black. In this peripheral species, however, it reputedly is red/red (Hoffman 1967). The disjunct Chattahoochee population of *rileyi* liès just north of red/red forms of *australis (Cheiropus),* in which the southernmost population also is red/black. Thus, there may be two disjunctions here, that in *rileyi* and that in the red/black pattern. If the latter disjunction exists it may be a relict of a once more widespread distribution of this character state, but it might also be convergent.

The disjunct populations of *rileyi* represent one of three instances in *Sigmoria s. lat.* of non-divergence among conspecific allopatric populations; the others obtain in *australis (Cheiropus)* and *stenoloba (Sigmoria).* The main population of *rileyi* is in piedmont Georgia, and satellite populations occur about 100 and 200 miles west in Lee and Jefferson counties, Alabama. Hoffman (1967) considered that in Lee County to be a distinct geographic race and predicted eventual discovery of material in the gap. However, the hiatus has been explored reasonably thoroughly at the time of year known populations are extant, and the gap appears to be real. Gonopods of all populations are practically identical, and subspecific status is unwarranted.

The acropodites of *rileyi, abbotti, bipraesidens,* and *robusta* in Georgia and South Carolina are massive and heavily sclerotized, and in this respect they are convergent with those of *crassicurvosa* and *pendulata (Falloria)* in central Tennessee. Individuals of the latter species even display thick subterminal acropodal lobes similar to those on the outer surfaces of the peaks and distal zones in *rileyi* and *abbotti.* The lobes are not homologous, however, as those in *rileyi* and *abbotti* represent modified lateral flanges, and the ones in the Tennessee species are extraneous and located on the medial surfaces. *Sigmoria (Falloria) fumimontis,* in the Great Smoky Mountains of eastern Tennessee, also has a heavy acropodite but the general configuration is more reminiscent of *latior (Sigmoria).* This also is convergence, because the narrow medial flanges, medial tilting of the peak, and divided prefemoral process clearly assign *fumimontis* to the *translineata* group *(Falloria).*

Hoffman (1967) and Whitehead (1972) proposed dispersal hypotheses to account for distributions of species of *Cleptoria,* but as with *Croatania* they are inappropriate because the animals are insufficiently vagile. These hypotheses did not account for *shelfordi, arcuata,* and *robusta,* but they incorrectly included *divergens (Cheiropus).*

Cheiropus. — This major component does not form a neat, definable group and is difficult to relate to the other subgenera. However, an undeniable transformation series links *stibarophalla* to the progressively more derived taxa formerly assigned to the separate genera *Prionogonus* and *Cheiropus* (Shelley 1982, 1984a), and the overall distribution of the subgenus provides an explanation for the relationships and distribution of *australis.* Both distributions and characters of the *planca* group, formerly the sole constituent of the genus *Cheiropus* (Shelley 1984a), seem superimposed upon rather than part of the generic mosaic, and our interpretations may need perceptive scrutiny in the future. We recognize ten species arrayed among the *australis* (#32), *divergens* (#33-34), *haerens* (#35-37), and *planca* (#38-41) species groups: *Cheiropus = australis + (divergens + (haerens + planca))* groups, mapped in figure 151.

The monobasic *australis* group has one of the three species in the genus with disjunct populations — one in coastal South Carolina and Georgia, one in south-central Alabama, and an intermediate one spanning the Chattahoochee River in southwestern Georgia, southeastern Alabama, and adjacent Florida. The latter two populations are approximately 40 miles apart and may prove to be connected, although appropriate habitats have been investigated without success. However, the central and eastern populations are so far apart as to virtually preclude extant linkage. Gonopods in all three areas vary within the same limits, and the populations are clearly con-

specific. The only curious character anomaly is in color pattern, with extreme southern representatives of the central population red/black rather than red/red.

Superficially, *australis* most resembles *stibarophalla,* at the opposite range extreme of *Cheiropus.* If *australis* is sister to the rest of the subgenus, this similarity may be explained as ancestral, and so may be the geographic separation of the similar elements. Moreover, an explanation for the disjunct populations arises from the same reasoning. They once were connected in the north and subsequently displaced by other forms of *Cheiropus* and/or *Cleptoria.* However, there is no good synapomorphy for the sister lineage, unless comparatively massive gonopods in *stibarophalla* and *divergens* is so considered. We adopt this scenario for explanatory purposes and erect a separate species group for *australis.*

The next vicariance in *Cheiropus* occurred in the north, separating the conservative *divergens* group *(stibarophalla,* #33, and *divergens,* #34) from those that developed acropodal solenomerites. Again, there is no precise autapomorphy for the *divergens* group, formed for vicariance reasons. If *stibarophalla* is the conservative gonopodal type from which other *Cheiropus* arose, geographic connections to them make sense only if *stibarophalla* and *divergens* shared common ancestry because of the relative geographic position of *stibarophalla.* Otherwise, the range of *divergens* represents a discontinuity between those of the *haerens* and *planca* groups.

One interesting feature of the *divergens* group is that the species *divergens* separates the ranges of *stenogon* and *disjuncta (Sigiria),* and proximal populations of all three taxa tend to be dark or purplish in markings. These are the only congeners so marked, and we consider this still another example of "incomplete synapomorphy". Mimetic convergence is unlikely, since the ranges of the three taxa are allopatric rather than sympatric. The gonopods of *divergens* are sufficiently unlike those of the other two species to suggest close relationship.

The *haerens* group *(Prionogonus sensu* Shelley 1982) has a relatively feebly developed solenomerite intermediate between the absence of such a structure in the *divergens* group and the well developed one in the *planca* group. It also is defined by the autapomorphous row of spurs on the outer surface of the basal zone. This feature is unique among xystodesmids and not homologous to modifications of this region in the *tuberosa (Falloria),* *rileyi (Cleptoria),* and *catawba (Croatania)* groups. The species geographically most proximal to the *planca* group is *thrinax,* which in general gonopodal form also is structurally most similar to the most proximal member of the *planca* group, *agrestis.* The *haerens* group includes three parapatric species *(haerens,* #35; *divaricata,* #36; and *thrinax,* #37) with

small geographic ranges, and, like the *australis* and *divergens* groups, it is part of the cohesive generic mosaic.

The *planca* group *(Cheiropus sensu* Shelley 1984a) includes four allopatric, more or less disjunct species so strongly differentiated from one another that three generic names have been associated with them. However, they lack obviously "sigmoid" gonopods, clearly an apomorphic condition. Also, an overall west to east clinal trend toward increased acropodal serration which persists independent of speciation is manifested in proximal populations of *agrestis* (#38), *serrata* (#39) and *planca* (#40) (Shelley 1984a). Moreover, *planca* is structurally intermediate between *serrata* and *persica* *(#41)*. Thus the *planca* group = *agrestis* + *(serrata* + *(planca* + *persica))*.

This species group weakens our generic hypothesis for *Sigmoria*. Not only is it differentiated by having secondarily curvilinear rather than "sigmoid" gonopods, but its distribution broadly overlaps that of various other southern members of the genus. Sympatry occurs within *Cheiropus* itself, between *serrata* and the syntopic eastern population of *australis,* and also between *agrestis* and two species of *Cleptoria.*

Sigiria. — This subgenus (Figures 151-152, areas 42-55) has two major subunits which are geographically contiguous but structurally disconnected by divergent forms, the *rubromarginata (#42-52)* and the *stenogon (#53-55)* species groups.

The *stenogon* group includes three geographically associated species, *stenogon (#54)*, *areolata* (#53), and *disjuncta* (#55). Of these, *disjuncta* is anatomically similar to *nigrimontis* (#46-49) and formerly was grouped with it (Shelley 1981a). However, the course of the prostatic groove differs, the color is purple/purple as in the most proximal populations of *stenogon,* and its range is separated from that of *nigrimontis* by *stenogon* and *areolata,* and species of the *rubromarginata* group. The adjacent species *areolata* and *stenogon* diverge in gonopodal features from *disjuncta.* Thus, the *stenogon* group = *disjuncta* + *(stenogon* + *areolata).*

The polytypic *nigrimontis* is structurally and geographically intermediate between the forms related to *rubromarginata* and *inornata.* Specifically, one may trace gradients in gonopod configurations from *nigrimontis* via *sigirioides (#50)* to *inornata* (#52) and *truncata* (#51), and via *triangulata* (#45), *rubromarginata* (#42), and *austrimontis* (#43) to *whiteheadi* (#44). In the Toe River Valley fauna, *inornata* occurs in the headwaters and therefore at a geographic extreme, and although the geographically intermediate *truncata* is more highly derived in gonopodal features, it shows clearer evidence of past continuity with *inornata* than with *sigirioides.* We have found no satisfactory dichotomous resolution of relationships among members of the *rubromarginata* group.

An instance of geographic discontinuity occurs in the *rubromarginata* group among taxa which should be clinally continuous. *Sigmoria rubromarginata* is restricted to the Blue Ridge Province of North Carolina and Tennessee, and the main population of *austrimontis* is found in the South Mountains, an inselberg chain in the western Piedmont Plateau. Their chief difference involves the distal zones, that of *austrimontis* being twisted mediad to reveal the surfaces of the medial and lateral flanges in medial view, while that of *rubromarginata* faces anteriad to reveal only the edge of the medial flange in this perspective. The range of the South Mountain form is contiguous in the western Piedmont and Blue Ridge escarpment with more variable ones that bridge the anatomical gaps. The latter populations of *austrimontis* have features that suggest intergradation with *rubromarginata,* but the taxa are disjunct by about 30 miles and are considered reproductively isolated. On the Blue Ridge Front in Virginia, *whiteheadi* occurs some 120 miles north-northeast of the nearest population of *austrimontis,* at Morganton, Burke County, North Carolina. Also, *whiteheadi* has yellow stripes instead of red, and the gonopodal resemblance between it and *austrimontis* is not as close as that between the latter and *rubromarginata. Sigmoria (Sigiria) whiteheadi* and *austrimontis* might seem to represent an eastward extrusion into an area between the ranges of *Dixioria* and *Croatania* that should otherwise be occupied by *Sigmoria s. str.,* but the supposed range extrusion violates the underlying hypothesis of simple vicariance partitioning. Rather than *Sigiria* plus *Falloria* as the basal sister element in the genus (Figure 154), that element should be either *Rudiloria* plus *Dixioria,* or *Croatania* plus *Cleptoria.* Resulting vicariance schemes appropriately place *Sigiria* between the ranges of *Dixioria* and *Sigmoria.*

Sigiria includes three yellow/yellow taxa — *areolata, inornata,* and *whiteheadi* — that are neither geographically nor structurally contiguous with one another. This coloration is found among members of several other eastern subgenera and is more probably an "incomplete synapomorphy" than an instance of convergence. Within *Sigiria,* however, this coloration is plesiomorphous. In *whiteheadi,* it is relictual in comparison to the syntopic yellow/black *l. latior (Sigmoria).* In *inornata,* the condition is variable, and, though we lack details, we predict that the populations most proximal to *truncata* are the ones that are red/red. *Sigmoria (Sigiria) inornata* occurs in headwater areas of the Toe River Valley, and its westernmost, downstream populations most resemble *truncata* in gonopodal characters by having longer and flatter peaks, and shorter distal zones. In *areolata,* an obvious sister to *stenogon,* the color is stable so far as known, but the

nearest populations of *stenogon* tend to be red/red unlike the purple/purple ones farther south, so that there is a stepped clinal continuum.

Although the *stenogon* group is closely allied geographically and structurally with the *rubromarginata* group, there is no obvious synapomorphy. Therefore, these may not truly be sister groups. Shelley (1981a) allied *nantahalae* (here placed in *Falloria*) with *stenogon,* as the two species then considered to represent the *stenogon* group. We assume that the resemblances were ancestral. This satisfies our premise that *nantahalae* is the sister element within *Falloria,* which despite diversity apparently is truly monophyletic. However, we are not certain that the *stenogon* group is not directly sister to *Falloria* rather than to the rest of *Sigiria.* Thus of the eight subgenera, *Sigiria* is the one least likely to be monophyletic.

Falloria. — This subgenus, (Figures 151-152, areas 56-73) consists of 18 species arrayed among eight species groups. The lineage is defended by geography (proximal only to *Sigiria),* linkages via transformation series, and apomorphous red/blue coloration. No other congeners have this bicolored pattern, which we presume is energetically expensive to acquire and therefore unlikely to be convergent. However, sympatric species of *Brachoria* also display the pattern, which we think represents mimetic convergence rather than "incomplete synapomorphy." In either case the coloration appears to be conserved by mimetic pressure. Two geographically peripheral species, white/white *leucostriata* (#57) and red/white *nantahalae* (#56), have color patterns unique in the genus. Both occur in areas not occupied by red/blue *Falloria* or *Brachoria,* and the absence of mimetic pressure may explain the absence of blue metatergal stripes.

The postulated sister group to *Falloria* is *Sigiria,* particularly the *stenogon* group, which is the basis for out-group comparisons. Northward, where species of *Falloria* are parapatric with those of the *rubromarginata* group, there is abrupt structural discontinuity. Our hypothesis of species group relationships is *Falloria = nantahalae + (leucostriata + (aphelorioides + (translineata + ((tuberosa + (bidens + picapa)) + mimetica)))).* This hypothesis is derived from the following considerations.

Aside from derived color pattern, the monobasic *nantahalae* group (#56) lacks gonopodal flanges. The ancestor of its sister group is postulated to have had a sort of hood on the peak of the acropodite.

The *leucostriata* group *(xerophylla,* #58, and *leucostriata,* #57) retains a short process on sternum 4, and its species are disjunct but gonopodally similar. The disjunction is explicable via vicariance partitioning. Its sister group is postulated to have had a medium process of sternum 4 ancestrally.

The monobasic *aphelorioides* group (#59) has a looped acropodite. Its sister group is postulated to have had an enlarged prefemoral process ancestrally.

The ancestor of the *translineata* group had a forked prefemoral process, whereas the ancestor of its sister lineage is postulated to have had the peak of the acropodite dentate ancestrally. The more eastern, Blue Ridge species *(translineata, lyrea, fumimontis,* and *ainsliei,* #60-63) had a more massive acropodite. The more western, Cumberland Plateau ones *(forficata, houstoni,* and *abbreviata,* #67-69) diverged into an easterly form with the process of sternum 4 lengthened and westerly forms in which it was shortened. Therefore, the *translineata* group = *((fumimontis + translineata) + (lyrea + ainsliei)) + (forficata + (houstoni + abbreviata)).*

Relationships among the *bidens, tuberosa, picapa,* and *mimetica* groups are more obscure. In the *bidens* group, the prefemoral process is more or less swollen, with the process of sternum 4 moderate in *bidens* (#64) but shortened in *prolata (*#65). In the Cumberland Plateau of Tennessee, the monobasic *picapa* group (#70) has the process of sternum 4 shortened and shares certain acropodal features with *prolata* of the *bidens* group, so the two groups are sisters. In the Blue Ridge, the *bidens* and *tuberosa* groups are not linked by a satisfactory synapomorphy, but by geographic inference. In the monobasic *tuberosa* group (#66), the prefemoral process is short and the process of sternum 4 is lengthened, in addition to various other distinctive features. In the Nashville Basin, the *mimetica* group has the process of sternum 4 shortened, and it is divergent in having greatly reduced prefemoral processes and massive acropodites in two species. Despite their divergences and disjunctions, the *tuberosa, bidens, picapa,* and *mimetica* groups appear readily interpreted as a once continuous northern vicariad.

The *mimetica* group *(mimetica,* #71, *crassicurvosa,* #73, and *pendulata,* #72) includes a curious population. One sample resembling the two eastern species, *pendulata* and *crassicurvosa,* was found in the eastern part of the range of the westernmost species, *mimetica.* The gonopods of *mimetica* are considerably thinner than those of the other two species (compare figures 111, 117, 123) and are homogeneous throughout the range. However, the above exception has a thicker acropodite with slightly swollen areas suggestive of lobes (Figures 113-114). It may represent a relict of a former connection between *mimetica* and *crassicurvosa,* and it also suggests that the three taxa of the *mimetica* group may be conspecific. The specimens were collected in 1957, and since then the eastern range periphery of *mimetica* and the area between the species has been thoroughly searched without finding more individuals. Consequently, the status of this population is uncertain, and it may be extinct. The massive gonopods of *crassicurvosa* and *pendulata* are synapomorphous. Thus, the *mimetica* group = *mimetica* + *(crassicurvosa + pendulata.)*

We propose the following vicariance sequence within *Falloria*. The first vicariance occurred on the southeastern front of the Blue Ridge, separating *nantahalae*. The second separated an eastern *leucostriata* group. The third segregated *aphelorioides* at the southern end of the Blue Ridge, and the fourth caused a south/north separation of the *translineata* group from the *tuberosa, bidens, picapa,* and *mimetica* groups.

This vicariance scheme produces some geographic quirks, notably in disjunctions between the Nashville Basin, Cumberland Plateau, and Blue Ridge. However, it also supplies a plausible explanation for the disjunct ranges of *xerophylla* and *leucostriata*. They are so similar in gonopodal characters that they must once have been continuous, but they now occur at opposite ends of the rugged southern Blue Ridge Mountains and are separated not only by distance and terrain but also by numerous congeners. Here, extinction of intermediates may have been caused by range expansions of other taxa, as suggested by the relatively large ranges of two intervening eastern species, *nantahalae (Falloria)* and *rubromarginata (Sigiria)*.

In *prolata,* isolated in a small pocket of the GSMNP near Gatlinburg, Tennessee, the distal zone curves sublaterad from the peak and is not coplanar with the basal zone. It is similar to that of *picapa* in the Cumberland Plateau and markedly different from the curvatures in *bidens* and the more southerly forms of the *translineata* group, in which the two zones are coplanar. The boundary between *prolata* and *bidens* in the Roaring Fork Nature Trail section of the GSMNP is sharp, as the latter occurs along the more southern entrance road and the former along the more northern exit road. This southern population of *prolata* has a mildly globose prefemoral process characteristic of *bidens* (compare figure 83 with Shelley 1981a, figure 80), unlike the northern, Greenbrier populations (Figures 79-82). The resemblance of the prefemoral process with *bidens* links only the most proximal populations, whereas the acropodal resemblance with *picapa* occurs throughout the range. Thus, the distal zone curvature of *prolata* and the bifurcate prefemoral process of *forficata* form evidence of former links between the Blue Ridge and Cumberland faunas.

Geographic factors indicate that the long sternal processes of *forficata* in the Cumberland Plateau, *tuberosa* in the Great Smoky Mountains of North Carolina, and various piedmont South Carolina species of *Croatania* and *Cleptoria,* represent convergence (see Table 2). *Sigmoria (Falloria) forficata* is separated from *tuberosa* by about 90 miles of the most rugged mountains in the southeast, and some 70 miles and more mountains segregate the latter from the piedmont forms.

In the Blue Ridge, *aphelorioides* has a circular acropodite similar to that of *ainsliei,* but it is placed in a separate species group because the prefemoral process is undivided. Their distributions, moreover, are separated by other species of the *translineata* group. Hence, their looped acropodites probably are convergent, as they also are with *trimaculata (Rudiloria)* and the genus *Apheloria.*

SUBGENERIC RELATIONSHIPS. — Here, we attempt to relate the subgenera of *Sigmoria,* discussed above and mapped in figure 153. We have no satisfactory character state nor transformation series to define the genus *Sigmoria* as monophyletic, but it is defined by its geographic cohesiveness. It has geographic properties similar to those of a single species. When species diverge, there is no theoretical need for both members of a sister pair to be defined by autapomorphies. Here, this applies at the generic level between the sister genera *Sigmoria* and *Deltotaria,* wherein the latter is defined by a satisfactory synapomorphy and represents a now independent overlay in the southern part of the former's range. The sister relationship of these two genera, as discussed under generic relationships later, is postulated on both geographic and structural grounds. We consider slender gonopodal form in the montane *D. brimleii* and in sympatric species of *Falloria* and *Sigiria,* and robust gonopodal form in the piedmont *D. lea* and in species of *Croatania* and *Cleptoria* in that region, evidence of past connections.

Problems with the preliminary subgeneric hypothesis. — The subgeneric arrangement used throughout this paper reflects a clockwise, radial arrangement from *Rudiloria* in the north to *Falloria,* based on the preliminary cladistic hypothesis shown in figure 154. This unsatisfactory, basally trichotomous arrangement specifies an east/west separation between the *Croatania/Cleptoria* and *Falloria/Sigiria* lines, with the geographically intermediate and more southern *Cheiropus* unassigned. The eastern lineage occupied the northern Appalachians and eastern piedmont, and the western lineage occupied the southern Appalachians and Cumberland Plateau. The eastern lineage divided into northern (*Rudiloria/Dixioria*) and southern components, the latter next into eastern (*Sigmoria*) and western (*Croatania/Cleptoria*) lineages.

Superficial gonopodal similarities between sympatric members of *Deltotaria* and *Sigmoria* formed one reason for a basal dichotomy separating *Croatania* and *Cleptoria* to the east from *Falloria* and *Sigiria* in the west. *Cheiropus,* which is geographically intermediate between these presumed sister pairs, does not bear conspicuous relationship to either.

Reasons for linking *Rudiloria, Dixioria,* and *Sigmoria s. str.* to *Croatania* and *Cleptoria* rather than to *Falloria* and *Sigiria* arose principally from the

geographic distributions of certain character states and postulated "incomplete synapomorphies" in the lengthened process of sternum 4 and the loss of metatergal stripes. In turn, *Sigmoria s. str.* seemed better tied to *Croatania* and *Cleptoria* than to *Rudiloria* and *Dixioria,* as judged prin-
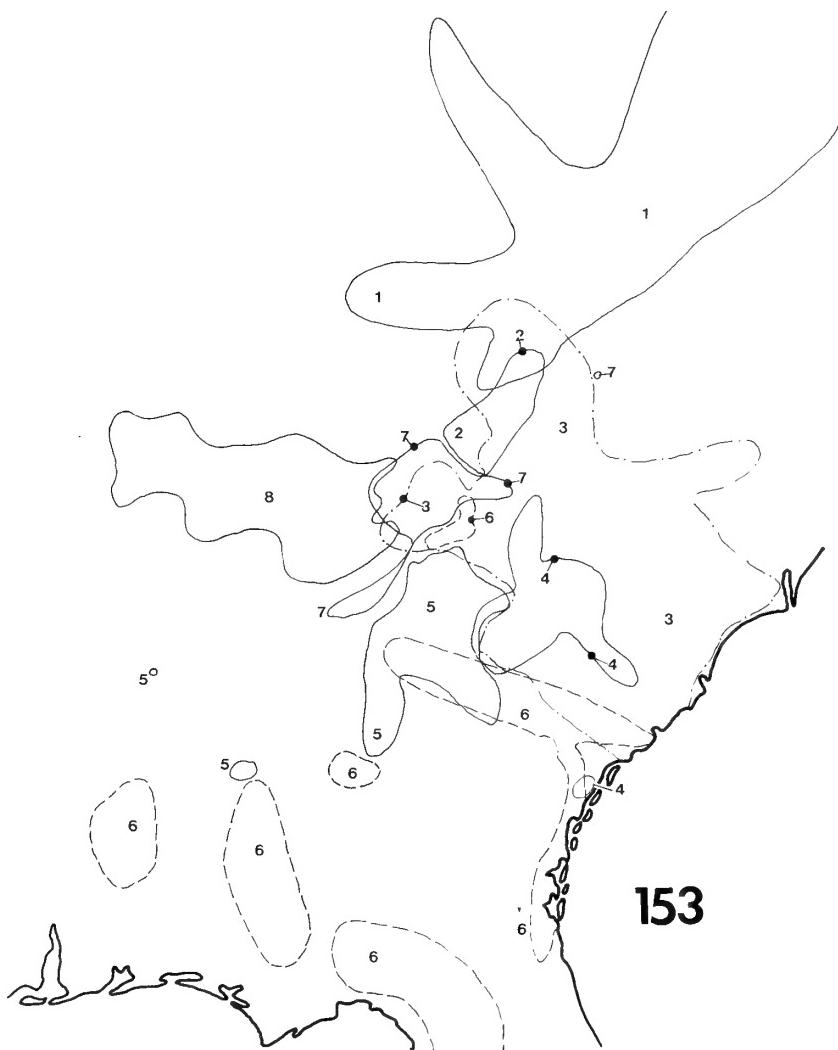
FIG. 153.   Distributions of the subgenera of *Sigmoria.*   1, *Rudiloria;*   2, *Dixioria;*   3, *Sigmoria;*   4, *Croatania;*   5, *Cleptoria;*   6, *Cheiropus;*   7, *Sigiria;*   8, *Falloria.*

cipally from some gonopodal similarities in *arcuata (Cleptoria)* and *quadrata (Sigmoria).*

This scenario is faulty in the following respects:

1. *Falloria* and *Sigiria* are allied, but it is not clear that *Sigiria* is monophyletic. *Falloria* might be directly allied to the *stenogon* group of *Sigiria,* but we found no compelling reason why the *rubromarginata* group might not be linked with *Sigmoria* rather than with *Falloria.* Nonetheless, we provisionally accept *Falloria* and *Sigiria* as true sister groups.

2. We accept *Croatania* and *Cleptoria* as sister groups based on synapomorphies. The argument for linking *Sigmoria* with *Croatania/Cleptoria* contradicts the character argumentation for recognizing basal
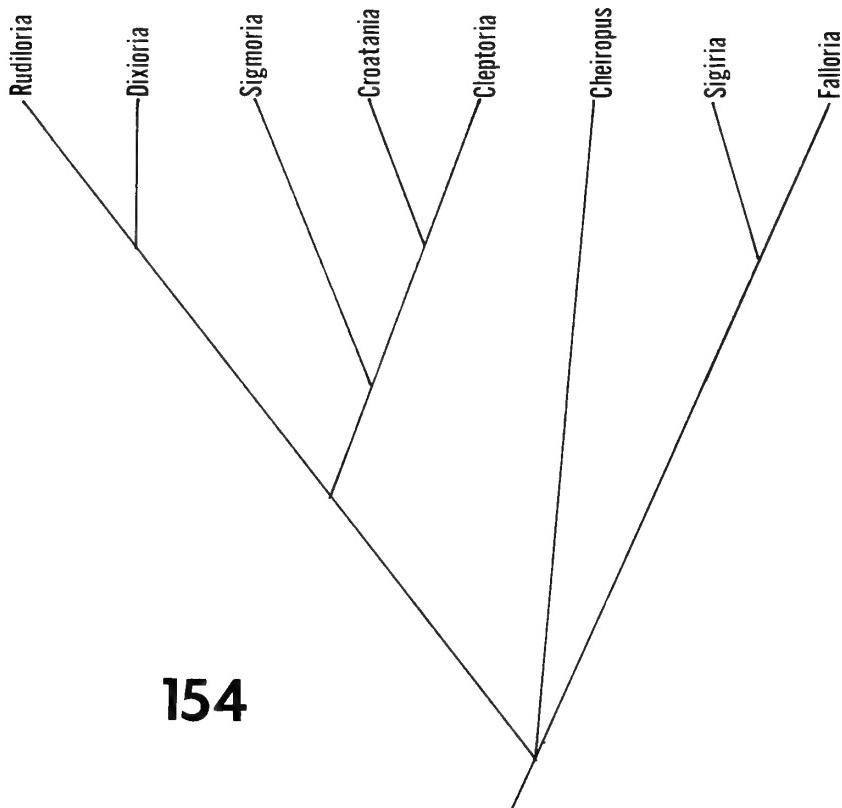
FIG. 154.   Relationships among the subgenera of *Sigmoria*, preliminary hypothesis.

Falloria/Sigiria and *Croatania/Cleptoria* lineages, because it specifies a reversal in gonopodal form from robust to slender, convergent upon that in *Sigiria*.

3. There are evident structural linkages of *Sigmoria* with *Sigiria* and/or *Cheiropus,* and either or both are geographically plausible. The position of *Cheiropus* is enigmatic, yet there are reasons to link it with *Sigmoria*. However, the ensuing hypothesis would have the combined distributions of *Cheiropus* and *Sigmoria* encircling those of *Croatania* and *Cleptoria,* an improbable vicariance scheme.

4. We accept *Rudiloria* and *Dixioria* as sister groups based on synapomorphy. However, proximal taxa of *Dixioria* and *Sigiria* have gonopods sufficiently similar that convergence is implausible. This presents a circular argument, if *Rudiloria* and *Dixioria* are said to have arisen from a lineage which ancestrally had massive gonopods.

5. The northeastward extension of *Sigiria* via *austrimontis* and *whiteheadi,* which separates the ranges of *Rudiloria/Dixioria* from those of *Croatania/Cleptoria,* represents an unnecessary argument for range dispersal made still more implausible by the large gap between *austrimontis* and *whiteheadi.* It can be avoided if *Rudiloria/Dixioria* is considered a basal sister element or otherwise separated from a *Croatania/Cleptoria* lineage. Consider the pizza pie analogy. No matter how irregular the slices, the pie does not actively slice itself. Thus, the postulated range extrusion of the *rubromarginata* group involving *austrimontis* and *whiteheadi* would be unsatisfactory even if there were a clear, extant continuum between the two.

Resolution of the problems. — If we accept *Falloria/Sigiria, Rudiloria/Dixioria,* and *Croatania/Cleptoria* as monophyletic groups, we need to select an appropriate dichotomous vicariance scheme for just five slices. There are 105 possible schemes, but many are geographically untenable as shown by figure 155. For instance, the sister of *Rudiloria/Dixioria* must either be or at least include *Falloria/Sigiria* to account for geographic proximity.

Neither *Cheiropus, Croatania/Cleptoria, Falloria/Sigiria,* nor *Sigmoria* alone represent plausible first cuts, because their distributions are wedge shaped. Hence, the first cut must have been *Rudiloria/Dixioria,* if we assume that one group is sister to the other four. If two groups are sister to the other three, the ones that need consideration are the following. For *Rudiloria/Dixioria,* the only possible pairing is with *Falloria/Sigiria,* and the only plausible triplet arrangement would include *Sigmoria.* For *Croatania/Cleptoria,* linkage could be with *Cheiropus* and/or *Sigmoria.*

An initial separation of *Cheiropus* and *Croatania/Cleptoria* from the rest of the genus based on ancestrally massive versus slender gonopods is geo-

graphically plausible, but the groups are divergent from one another and *Cheiropus* shows affinity elsewhere in the genus. In an initial separation of *Rudiloria/Dixioria* and *Falloria/Sigiria* from the rest of the genus, neither
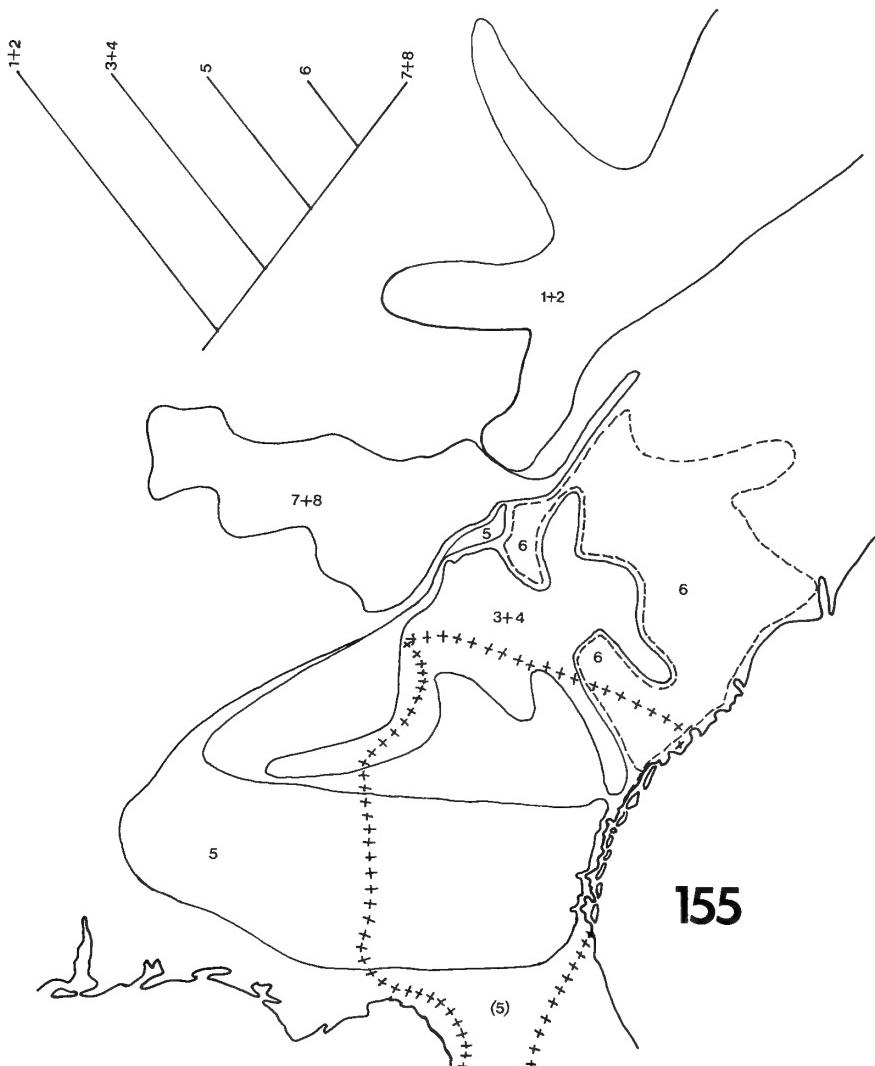
FIG. 155.   Vicariance map and cladogram for the subgenera of *Sigmoria,* numbers as in Fig. 153. The Jefferson Co., AL, record of *rileyi (Cleptoria)* and areas of secondary sympatry of *latior (Sigmoria)* are omitted. 1 + 2, *Rudiloria + Dixioria;* 3 +4, *Croatania + Cleptoria;* 5, *Cheiropus* [(5), *planca* group]; 6, *Sigmoria;* 7 + 8, *Sigiria + Falloria.*

lineage in the basal dichotomy is supported by a satisfactory autapomorphy. We reject these hypotheses.

We propose *Rudiloria/Dixioria* as sister to the rest of the genus. This is the most probable, geographically simple arrangement and is based on the most satisfactory autapomorphy, although for one lineage only: gonopod orientation in *Rudiloria/Dixioria*. Slender gonopods in *Rudiloria/Dixioria* and proximal *Sigiria* represent the ancestral condition, not convergence, and there are no detailed residual linkages with other groups such as are implied between *Croatania/Cleptoria* and *Sigmoria*. This arrangement also implies convergence rather than "incomplete synapomorphy" in the lengthened process of sternum 4 and color pattern. Thus, the continuum of the *rubromarginata* group of *Sigiria* via *austrimontis* to *whiteheadi* divides the lengthened process of sternum 4 of *Rudiloria/Dixioria* from those of *Croatania/Cleptoria* and southern members of *Sigmoria*. Moreover, the color pattern involving lack of metatergal stripes may represent mimetic convergence, as the distribution of *l. latior (Sigmoria)* completely overlaps that of *Dixioria* rather than being contiguous.

If *Rudiloria/Dixioria* is sister to the rest of the genus, then just four groups and 15 dichotomous arrangements remain. Only *Croatania/Cleptoria* is a geographically and structurally suitable basal element. As in *Rudiloria/Dixioria,* there is an acceptable ancestral autapomorphy for *Croatania/Cleptoria,* the spine or irregular notching on basal zone, but not for the sister lineage.

This leaves just three groups and three arrangements. Our resolution of these is based partly on geography and partly on divergence. *Cheiropus* has elements which are the least similar, perhaps in part reflecting ancestral geographic variations in the genus. Where geographically proximal to *Falloria/Sigiria,* there is little structural resemblance. Geographic connections with *Sigmoria* are in part dissected by the range of *Croatania/Cleptoria,* and where the ranges overlap, as with *l. munda (Sigmoria)* and the *divergens* and *haerens* groups *(Cheiropus),* gonopods are too dissimilar to imply close common ancestry. In contrast, gonopodal similarities of proximal elements of *Sigmoria* and *Falloria/Sigiria* are much stronger.

Relationships among the subgenera. — Our revised cladistic hypothesis (Figure 156) is: genus *Sigmoria = (Rudiloria + Dixioria) + ((Croatania + Cleptoria) + (Cheiropus + (Sigmoria + (Sigiria + Falloria)))).*

This hypothesis represents our best estimate of vicariance partitioning of the subgenera. In the absence of a suitable synapomorphy scheme, which we think does not exist, it is perforce based principally on the geographic distributions of the taxa and their character states considered together. It does not resolve the problems of undefined monophyly of *Sigiria* nor defini-

tion of the lineage *Sigiria/Falloria*. However, the only plausible geographic linkage for *Falloria* is with *Sigiria* (or a part of *Sigiria*, the *stenogon* group), and if *Sigiria* is not a natural group the only plausible alternative arrangement is to shift the *stenogon* group to *Falloria*.

Features of the hypothesis are the following:

1. The partitioning pattern (Figure 157) is coherent and sequential, requiring only minimal range alteration and secondary sympatry to achieve the present distributional pattern.
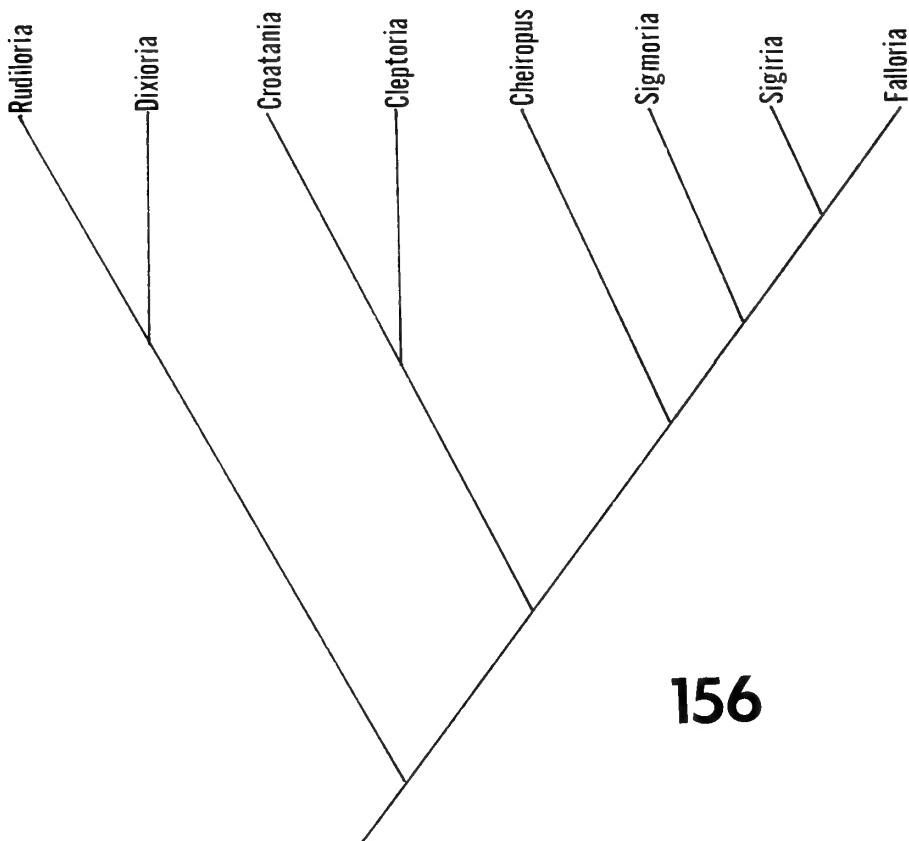
FIG. 156.   Relationships among the subgenera of *Sigmoria*, revised hypothesis.

2. The virtual encirclement of *Croatania/Cleptoria* by *Cheiropus* and *Sigmoria s. str.* is geographically illogical and thus probably secondary. Aside from the clearly secondary distribution of the *planca* group, the southern area of *Cheiropus* is represented only by the now disjunct populations of *australis*. That these may be recent immigrants is consistent with their lack of differentiation.

3. The gonopodal similarities between *Rudiloria/Dixioria* and *Sigiria* reflect ancestral similarity, not convergence. Length of the process of sternum 4 is not quite continuous from *Dixioria* to *Sigmoria*.

The ancestral similarity features implied by items 4-6, both somatic and gonopodal, are ones that cross indicated cladistic lines. We conclude that they are plesiomorphous, not apomorphous.

DISCUSSION. — Traditional cladistic analysis assumes that lineages are independent and definable by autapomorphies, and where apparent conflicts occur they are resolved by parsimony techniques. The traditional analysis is based solely on character information, *independent from* geography. Our first assumption must always be that a character based cladistic hypotheses is attainable, regardless of initial impressions. Even after realizing that *Sigmoria* was a geographic mosaic, we still attempted traditional analysis. It failed. Our initial attempts involved the taxa first reviewed by Shelley (1981a) and were based on color, body size, details of gonopodal structure, and even ecology. We found virtually complete noncongruence between all characters studied and could only conclude that *Sigmoria* as it then stood could not be monophyletic, despite patterns of geographic contiguity among character states. Parts of the puzzle seemed to be missing.

The conclusions about relationships reached in this paper need to be tested by rigorous cladistic analysis, but we contend that such analysis will require substantially more critical information such as might derive from facial chaetotaxy and comparative body chemistry. Nearly all of the characters and character conditions that we presently have for analysis are homoplasious.

Therefore, the key to solving relationships within *Sigmoria* is the realization that the genus is a geographic mosaic. Its autapomorphy is geographic cohesiveness; *Sigmoria* has the geographic properties of a species. Its minimal divisions, the species and subspecies, also are geographic entities, with allopatric and/or parapatric relations to other such divisions. Character states map in cohesive geographic patterns but are noncongruent with one another. The *only* way to analyze the mosaic based on presently available character data is to *include* geography.

In our analysis of major components, we combined geographic and cladistic inference to refute the null hypothesis that the genus *Sigmoria* was a continuum. We tested the subgenera as stationary vicariads in our analysis of relationships. In both cases, spatial configurations are the critical factor.
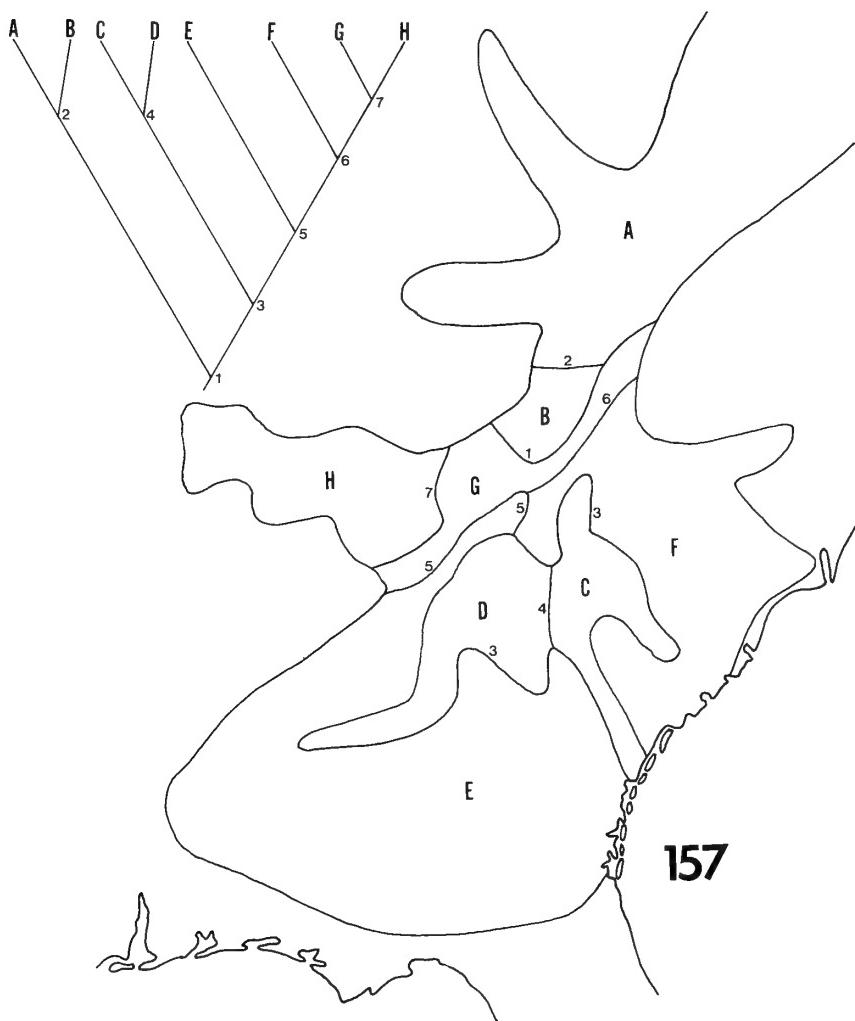
FIG. 157. Partitioning system and cladogram for the subgenera of *Sigmoria*. A, *Rudiloria;* B, *Dixioria;* C, *Croatania;* D, *Cleptoria;* E. *Cheiropus;* F, *Sigmoria;* G, *Sigiria;* H, *Falloria*.

In traditional cladistic analyses, both lineages of a sister pair are defined by autapomophies. However, in *Sigmoria,* rarely are both members of geographic pairs thus defined. This situation merely reflects the evolutionary history of the mosaic, which was created by simple vicariance partitioning. Both divergence and extinction are largely absent from the system. Though we were forced to use geographic distributions alone to determine sequencing, we are satisfied with the accuracy of the method although it lacks the persuasive force of traditional character analyses. The method should pertain to all tightly fitted allopatric/parapatric mosaics. For their resolution, major component analysis using both geographic and character distribution inference is the only recourse available. In *Sigmoria* it is easier to analyze cladistic (character) relationships within the subgenera than between them. These units are segments of the geographic whole, and thus their constituent parts are less divergent and demonstrate more obvious linkage patterns.

It is ironic that a thorough analysis of *Sigmoria* lends credence to the judgement by Hoffman (1958a) that it had become a "catch-all" genus. Now, it is much more so, because it has "caught" all relevant pieces of a biological mosaic. All of the subgenera, previously considered genera, represent only fragments of a single geographic entity. *Sigmoria* thus is larger than anyone previously imagined. What we now call *Sigmoria* is an enormous apheloriine mosaic complex that blankets eastern North America. We might speculate on its origin, how it came to cover so large an area, and the nature of the vicariance mechanisms, but the important fact is that vicariance did take place. Various ancestral character clines were irregularly fragmented to create the present picture. Extinctions and dispersals seem to have played a negligible role. What seems to be active, dispersalist speciation is only the passive result of vicariance. The animals do not actively explore new areas and environments. Instead, they remain in one place and eventually become isolated. The resultant localized populations are reflected in the phenotypes that we interpret as reproductive isolates.

The story of *Sigmoria* still may be incomplete. Other chapters may unfold when *Apheloria* and *Brachoria* are reexamined. Future workers may conclude that *Sigmoria* must be submerged under one of these older names, particularly *Brachoria,* although we think they form separate mosaics. The forms assigned to *Brachoria* have "sigmoid" acropodites that fall within the range of curvatures in *Sigmoria.* Published drawings show apparent medial flanges, teeth on the medial and undersurfaces of the peaks and distal zones, and various other acropodal modifications comparable to conditions found in *Sigmoria.* The cingulum on the outer surface of the acropodite, which we regard as autapomorphous for *Brachoria,* might real-

ly be of polyphyletic origin as it occurs at different relative positions. However, a test for homology may be possible by doing the same kind of major component analysis as we have done for *Sigmoria*.

We think *Sigmoria* can serve as an example in diplopodology of a geographic mosaic, a highly partitioned but still cohesive entity in which differentiation must be rapid. Problem groups, in which accurate delineation of species or genera is difficult, exist throughout the class. In the Polydesmida the xystodesmid genera *Rhysodemus* and *Nannaria* may have as many as 100 and 200 species respectively (Hoffman 1964, 1966, 1970), and the chelodesmid genus *Chondrodesmus* has over 40 weakly differentiated ones (Hoffman 1978b). In the Spirobolida, the Rhinocricidae is renowned for its internal confusion. Hoffman (1969, 1978b, 1979) suggested that these groups are in expanding phases of evolution and actively speciating. We agree that speciation is taking place, but we think it is accomplished passively through vicariance. These and such polydesmoid taxa as *Amplinus* and *Pycnotropis* (Platyrhacidae) and the phenotypically similar California xystodesmids *Xystocheir, Paimokia, Motyxia,* and *Amplocheir* (Xystocheirini) probably are other examples of large, complex mosaics with clines and gradients that have been randomly split by vicariance events, some of which are incomplete. In poorly vagile millipeds, dispersal probably plays only a minor role in the speciation process.

The insight on mosaics derived from *Sigmoria* should apply also to other animal groups with allopatric/parapatric patterns. For example, one may think of systems of isolated mountain peaks, caves, or sand dunes and their specialized beetle faunas. As with the Diplopoda, these mosaic patterns reflect inherent nonvagility. In more highly vagile animals, mosaic patterns may be dictated by extrinsic biotic factors, such as critical host plant associations or mimetic complexes. In such situations, the mosaic must be identified and its pieces analyzed, requiring detailed distributional information as has been compiled for *Sigmoria*. We have identified the shapes of its constituent basic pieces, the species and subspecies; analyzed the relative fits of these pieces to one another; and provided an internally consistent, working hypothesis of relationships for future workers to test. It remains for them to complete the analysis of the Apheloriini by applying these procedures to *Apheloria* and *Brachoria* and then to reexamine *Sigmoria* to determine if it should be submerged under one of these older names. To facilitate this process, we conclude with a review of the apheloriine genera, an analysis of their relationships as far as possible, and an analysis of the affinities among the four principle eastern xystodesmid tribes.

PART VII: THE GENERA OF THE TRIBE APHELORIINI
By Rowland M. Shelley

Tribe APHELORIINI Hoffman

Apheloriini Hoffman, 1979:158, 187.

Components: Apheloria Chamberlin, 1921; *Brachoria* Chamberlin, 1939; *Dynoria* Chamberlin, 1939; *Sigmoria* Chamberlin, 1939; *Deltotaria* Causey, 1942; *Furcillaria* Shelley, 1981.

Diagnosis. — Relatively flexible Xystodesminae of moderate to large size; midbody sterna broad and flat or with variable grooves or impressions, without elevations, caudal edges straight or only slightly produced, without lobes or spines; anterior tarsal claws of males normal, bisinuate; gonopods small to large; sterna connected by membrane only, without sternal remnant; coxae with or without variable apophyses arising on anterior sides, extending ventrad; prefemoral process present or absent, when present variably curved and elongate, often enlarged or subglobose basally, never acicular; telopodite usually entire, occasionally divided or with separate solenomerite, usually curving anteriad, anteriomediad, or mediad in sigmoidal, semicircular, or circular configurations, occasionally linear, usually twisted or with torsion at 1/4 to 1/3 of total length, resulting in crossing of prostatic groove from medial to lateral surfaces; cyphopods with variable receptacle.

Distribution (Fig. 158). — Eastern North America from northern New England to south-central Wisconsin (passing through southern Ontario and the lower peninsula of Michigan) south to Baton Rouge, Louisiana, southern Alabama and Mississippi, and just north of Tampa, Florida. Longitudinally, the tribe is known from the Atlantic seaboard from northern Florida to Virginia, New Jersey to Connecticut, and near the coast in Maine to southeastern Nebraska and eastern Oklahoma. The shaded area in figure 158 was determined from published records in Chamberlin and Hoffman (1958) and Keeton (1959, 1965) plus specimens I have personally collected or seen in museum and private collections. The contrast between the smooth northern and irregular southern boundaries is striking, but the northern distribution has not been as thoroughly studied and its evenness may reflect insufficient sampling. I also slightly extended the northwestern corner into southeastern South Dakota, since the presence of *Apheloria* at Omaha, Nebraska (see *Apheloria* account), suggests potential occurrence in riparian habitats farther north along the Missouri River.

Remarks. — This revised diagnosis incorporates no real changes from the original by Hoffman (1979), but it is substantially expanded to better

contrast the Apheloriini with the other major eastern tribes —
Rhysodesmini, Nannariini, and Pachydesmini (see Hoffman 1960, 1964;
Shelley 1984c). The date of proposal of *Deltotaria* is also corrected to 1942.

Just as colors and color patterns tend to cluster within *Sigmoria s. lat.,*
they also do within the *Apheloriini* as a whole and between tribes, and this
probably represents mimetic convergence. For example, populations of *l.
latior* and *stenoloba (Sigmoria)* with uniformly black metaterga occur sym-
patrically in Wilkes and Ashe counties, North Carolina, with forms of
Pleuroloma flavipes having the same markings, and as mentioned earlier
the various striped patterns in *Sigmoria s. lat.* tend to overlap areas where

FIG. 158.   Distribution of the Apheloriini.

they are also exhibited by *Dynoria, Furcillaria,* and *Brachoria.* I was repeatedly frustrated in searches for the subgenus *Falloria* in the Cumberland Plateau of Tennessee by the recovery of large numbers of red/blue forms of *Brachoria* and none or only a few of *Falloria.* For example, in a large series of red/blue forms from Rainbow Lake, Hamilton County, there were seven males of *B. hubrichti* Keeton and only one of *S. (F.) forficata.* This color pattern in *Brachoria* extends into Alabama approximately to Birmingham, but knowledge of its complete range must await revision of this genus and more field work in Kentucky. However, the extent of the red/red pattern can be reported and is shown in Figure 159. There are two large areas separated by a narrow gap in Piedmont, Georgia. One extends from eastern Tennessee through the Carolinas to piedmont and coastal Georgia, with a branch swinging northward into southeastern North Carolina, and the other begins in central and western Georgia, curves into southern Alabama, widens in a northerly direction to the northwestern corner and adjacent Mississippi, then angles to the Mississippi River. The actual northern and western limits in Alabama and Mississippi are uncertain because of inadequate knowledge of *Brachoria,* but from my limited personal experience these colors are displayed by forms in northern and central Alabama and northern and southwestern Mississippi. The area is extended to Baton Rouge, Louisiana, as *Brachoria* is now known to occur there (see *Brachoria* account) and these were the colors of a female I collected in 1980 in Claiborne County, Mississippi, along the Mississippi River between Vicksburg and Natchez, about 100 miles north of Baton Rouge.

Genus APHELORIA Chamberlin

Apheloria Chamberlin, 1921:232
Leptocircus Attems, 1931:67, preoccupied by *Leptocircus* Swainson, 1833; (Jeekel 1971).

Type species. — Of *Apheloria, Fontaria montana* Bollman, 1887, by original designation; of *Leptocircus, L. inexpectatus* Attems, 1931, by original designation.

Diagnosis (adapted from Hoffman 1978a). — Telopodite set subterminally on coxa, latter projecting distad *in situ* beyond base of prefemoral region; acropodite with torsion, in configuration of tight coil of around 340°, bent abruptly dorsad apically.

Ecology. — The species of *Apheloria* appear to have less specific habitat requirements than most of those of *Sigmoria s. lat.* and are somewhat

similar to *latior (Sigmoria)* in being ecological generalists. They occur under logs, rocks, and leaves in mixed deciduous forests as well as in many cove and stream environments. Thus in the Blue Ridge, Ridge and Valley, and Cumberland Plateau Provinces, one is more likely to encounter *Apheloria* on wooded hillsides than any other apheloriine genus, and it is often syntopic with the rhysodesmine genus *Cherokia.* With the exception of *latior,* *Apheloria* is encountered in disturbed and urban habitats to a much greater degree than any other member of the tribe.

Distribution. — The northern 2/3 of eastern North America from a line extending from central New York through southern Ontario, southern Wisconsin, and northern Iowa south to central Arkansas, northern Alabama, and northern South Carolina; longitudinally from along the Atlantic Ocean from southeastern North Carolina to central Connecticut west to eastern Oklahoma and southeastern Nebraska. A recent collection has established its presence on Bald Head Island off the coast of North Carolina.

Species. — Exact total unknown. Hoffman (1978a) listed 14 names that were based on specimens having gonopods identical or similar to those of *montana* and indicated that most were synonyms or at best had subspecific rank. However, another name has since been added to the list, as I reported (1980b) that *Julus virginiensis* Drury, 1770, was based on a form of
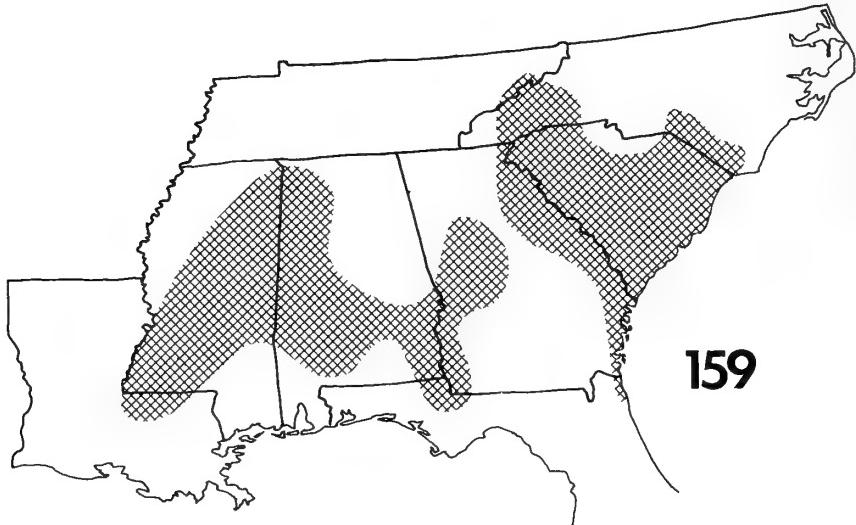
FIG. 159.   Approximate distribution of the red paranota/red metatergal stripe color pattern in the Apheloriini.

Apheloria. It is obviously much older than the other names and thus has taxonomic priority.

Remarks. — Since it is the oldest name in the tribe, taxonomic decisions in the Apheloriini may need modification when *Apheloria* is revised. However, I think it and *Brachoria* comprise separate mosaic complexes which overlie each other and *Sigmoria s. lat.* to varying degrees and thus are generically distinct. The species of *Apheloria* also have different ecological properties, a fact that seems taxonomically significant. Another factor that may warrant consideration is the size, shape, and variation of the process of the 4th sternum in males. As shown in Table 2, it varies greatly in *Sigmoria s. lat.* and knowledge of its condition in *Apheloria* and *Brachoria* may clarify affinities among the genera.

As a final note, I suggest that *Fontaria luminosa* Kenyon (1893) is refer- rable to *Apheloria*. Chamberlin and Hoffman (1958) listed the binomial under "uncertain generic position", and its identity has been an enigma. The type specimen(s) are lost, and the type locality is Omaha, Douglas County, Nebraska. According to Kenyon, the male genitalia curve "in- ward, forward, outward, and downward," a characterization applicable to *Apheloria* and how a non-specialist might describe the circular acropodite when viewed *in situ*. In August 1983 I found a xystodesmid sample from Omaha in the NMNH consisting of one male and three females labeled, "*Fontaria luminosa* (Type?)." Unfortunately, the gonopods of the male were missing, but from knowledge of xystodesmid distributions, only three species are potential inhabitants of eastern Nebraska — *Pleuroloma flavipes* Rafinesque (Shelley 1980b), *Semionellus placidus* (Wood) (Chamberlin and Hoffman 1958), and a form of *Apheloria* (Chamberlin and Hoffman 1958, plus knowledge I have derived from museum holdings). The specimens are not *P. flavipes* because they lack the diagnostic sternal lobes (Shelley 1980b), and they are much too large to be *Semionellus placidus*. By elimination they must be a form of *Apheloria* if the locality is correct, and the question mark concerned the designation as type, not the place of collection. I think Omaha must be considered accurate, and assign- ment to *Apheloria* is compatible with Kenyon's description. The matter can be finalized by collection of an adult male in the general vicinity of Omaha or Lincoln, where Kenyon (1893) reported a sight record. With the occur- rence of *Apheloria* in eastern Nebraska now fairly certain, its discovery can be reasonably predicted in riparian habitats along the Missouri River in southeastern South Dakota. The name, *luminosa,* also has priority for midwestern forms of *Apheloria,* being 38 years older than Attems' name, *inexpectatus.*

Genus BRACHORIA Chamberlin

Brachoria Chamberlin, 1939:3.
Tucoria Chamberlin, 1943b:17.
Anfractogon Hoffman, 1948:94.

Type species. — Of *Brachoria, B. initialis* Chamberlin, 1939, by original designation; of *Tucoria, Fontaria kentuckiana* Causey, 1942, by original designation; of *Anfractogon, A. tenebrans* Hoffman, 1948, by original designation.

Diagnosis. — Acropodite with torsion, bisected at various positions by distinct cingulum.

Ecology. — I have collected forms referrable to *Brachoria* in a variety of habitats. In western North Carolina they can be found in mixed deciduous forest and cove environments. In the Cumberland Plateau of Tennessee and Alabama they occur in the latter or along streams in the most moist spots available. Farther south in Alabama and in Mississippi, they occur only in deciduous environments along streams.

Distribution. — As shown by Keeton (1959) and Hoffman (1971), *Brachoria* extends in a northeast-southeast direction from a center of abundance in the Cumberland Plateau Province. It is known as far north as Fayette County, Pennsylvania (Carnegie Museum of Natural History), and southeastern Indiana; as far east as the Blue Ridge Front in McDowell County, North Carolina (Shelley 1979b); and as far south as Lee County, Alabama, and East Baton Rouge Parish, Louisiana (FSCA).

Species. — Twenty nine are now recognized, one with three subspecies.

Remarks. — I indicated (1979b) that a second revision of *Brachoria* was needed to consider the nomenclature changes since Keeton's revision (1959) and include newly collected material. Such a study is as important as a revision of *Apheloria,* and *Brachoria* could be assigned top priority because it has more species. Although defined by the acropodal cingulum, presumably an autapomorphy, I am not certain *Brachoria* is monophyletic because the location of the cingulum varies, suggesting independent evolution from two or more ancestral stocks. Thus, a synonym may have to be revived or a new genus proposed to accommodate some forms. These are matters that should be addressed in a second revision.

Genus DYNORIA Chamberlin

Dynoria Chamberlin, 1939:7.

Type species. — *D. icana,* Chamberlin, 1939, by original designation.

Diagnosis. — Acropodite without torsion, prostatic groove running entirely along medial surface; divided at 2/3-3/4 length into lateral tibial process and medial solenomerite branch.

Ecology. — My only field encounter with *D. icana* was in Oconee County, South Carolina, where I found it under a thick layer of leaves in a slight depression in an oak-hickory forest near Hartwell Reservoir (Shelley 1984b). It also occurs on the edge of the Blue Ridge Province, but there are no ecological notes on collecting labels. In Georgia, *D. medialis* is found in typical piedmont habitat, under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — Southeastern extremity of the Blue Ridge Province in North Carolina and Georgia, extending onto the Piedmont Plateau of western South Carolina, and the Piedmont and Coastal Plain of central and southwestern Georgia (Shelley 1984b).

Species. — Two, one in each of the above described regions.

Remarks. — *Dynoria* is the only apheloriine genus lacking torsion, and along with *Furcillaria,* one of only two with a distally divided acropodite. I indicated (1984b) that they comprise a separate evolutionary branch in the Apheloriini, but as shown in Figure 160, they actually represent distinct lineages because torsion constitutes a synapomorphy between *Furcillaria* and the other tribal components. I also proposed a dispersal mechanism for evolution of *Dynoria* and *Furcillaria,* but this scheme is inoperative. The animals are not sufficiently vagile for dispersal to be more than a minor factor in their evolution; instead, vicariance is operative.

Genus FURCILLARIA Shelley

Furcillaria Shelley, 1981c:953-955.

Type species. — *F. aequalis* Shelley, 1981, by original designation.

Diagnosis. — Acropodite with torsion, prostatic groove crossing to lateral surface near 1/3 length; divided at 2/3-3/4 length into lateral tibial process and medial solenomerite branch.

Ecology. — The species of *Furcillaria* occur under thin layers of leaves on relatively hard substrates near water sources.

Distribution. — A triangular area in the Piedmont Plateau of South Carolina between the Pacolet and Savannah Rivers, extending to the western tip of the state in Oconee County. The species are allopatric and occupy narrow bands within the generic range.

Species. — Three.

PART VIII. RELATIONSHIPS IN THE TRIBE APHELORIINI

By Rowland M. Shelley and Donald R. Whitehead

Shelley (1981a) deferred discussion of generic affinities of *Sigmoria* until taxonomic knowledge of the other apheloriine genera could be brought to comparable levels. This has since been done for all except *Apheloria* and *Brachoria,* so we now provide preliminary assessments of relationships among the genera and eastern xystodesmid tribes. Important recent works on the Rhysodesmini and Pachydesmini are those by Shelley on *Pleuroloma* (1980b) and *Dicellarius* (1984c). None has appeared on the Nannariini, but Hoffman (1964) presented a modern tribal diagnosis.

Out-groups used to infer plesiomorphic and apomorphic character states in the Apheloriini are the three other eastern xystodesmid tribes: Rhysodesmini, Pachydesmini, and Nannariini. For tribal comparisons, Rhysodesmini serves as the out-group; although well represented in the east, it also occurs from southern Texas and New Mexico to El Salvador, where it is the sole xystodesmid tribe. The only eastern species not included in these comparisons is *Semionellus placidus,* which is not a member of the endemic eastern tribal complex of Nannariini, Pachydesmini, and Apheloriini. A member of the Chonaphini and related to species in the Pacific Northwest (Hoffman 1979), it has a much more slender form than do other eastern xystodesmids, and its gonopods are divergent in having the acropodite simple and the prefemoral process strongly modified.

The Generic Hypothesis. — The following character statements document the generic hypothesis in figure 160: Apheloriini = *Dynoria + (Furcillaria + (Apheloria + Brachoria + (Deltotaria + Sigmoria))).*

1. *Presence or absence of gonopodal torsion.* In all apheloriine genera *except Dynoria,* the acropodite is twisted at 1/3 to 1/2 length, causing the prostatic groove to cross from the medial to the lateral surfaces. This is true even for the *planca* group of *Sigmoria,* wherein the structure is basically curvilinear. Conversely, all pachydesmines except *Dicellarius okefenokensis* and all rhysodesmines and nannariines lack torsion, and the entire course of the prostatic groove or nearly so is visible in medial view. Presence of torsion is therefore considered autapomorphous.

2. *Acropodite divided or undivided.* The acropodite is divided in *Dynoria, Furcillaria,* the Pachydesmini, and many taxa of the Rhysodesmini and Nannariini. An undivided acropodite is autapomorphous in other Apheloriini. An autapomorphous, lateral solenomerite in the *haerens* and *planca* groups of *Sigmoria* is not homologous with the apically divided acropodite.

From this point on, we have found no clear synapomorphies to specify sister group relationships. The following are generic features.

3. *Acropodal ground plan circular or "sigmoid."* The acropodite in *Apheloria* forms a tight, nearly circular coil. The acropodites of *Furcillaria, Brachoria, Deltotaria,* and most species of *Sigmoria* are basically "sigmoid." The nearly circular loops of *Sigmoria ainsliei, aphelorioides,* and *trimaculata* differ from those of *Apheloria* and are considered convergent. The only other known xystodesmid with coiled acropodites is the oriental genus *Parafontaria,* placed because of other characters in a separate subfamily by Hoffman (1979). The coiled acropodite of *Apheloria* is apomorphous if the genus belongs to a group excluding *Furcillaria* as specified by character 2 and if the "sigmoid" acropodite of *Furcillaria* is homologous to that of *Brachoria, Deltotaria,* and *Sigmoria. Apheloria* may be sister to *Brachoria + (Deltotaria + Sigmoria),* but we found no synapomorphy for them.

Dynoria · Furcillaria · Apheloria · Brachoria · Deltotaria · Sigmoria

5

4

3

2

1
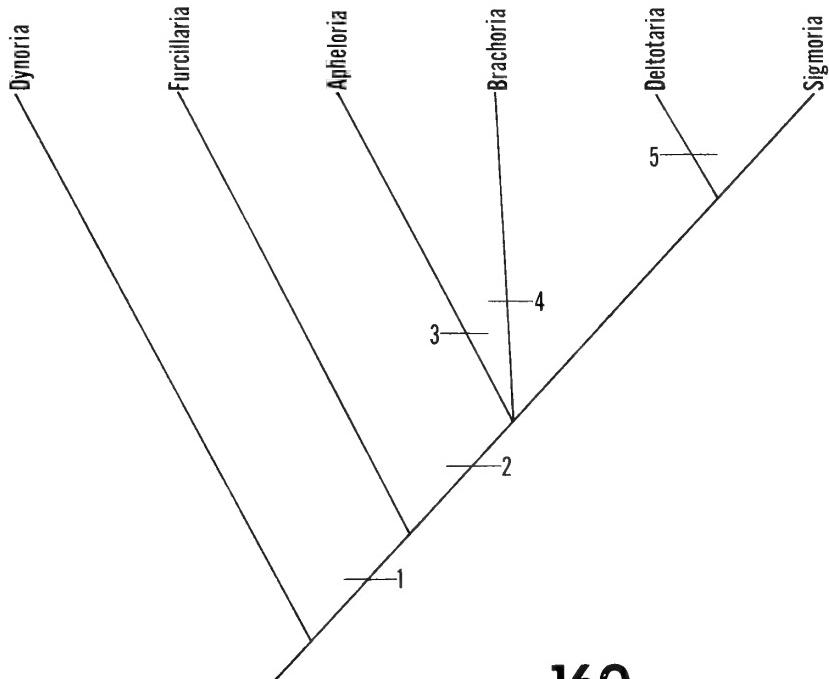
160

FIG. 160.   Generic relationships in the Apheloriini. The numbers refer to apomorphies discussed in the text.

4. *Presence or absence of a gonopodal cingulum.* A cingulum, or transverse depression on the outer surface of the acropodite stem, is unique to *Brachoria* and is considered autapomorphous pending review of this genus. The acropodite is set off from the prefemur by a cingulum in the rhysodesmine genus *Cherokia* (Hoffman 1960), but we know of no other xystodesmid genus with one on the acropodite blade in each component species.

5. *Presence or absence of a coxal apophysis.* An apophysis, or ventrally directed projection on the gonopodal coxa, is independently apomorphous in *Deltotaria, Pachydesmus,* and *Xystodesmus* (Hoffman 1956b, 1958b; Shelley 1984c).

Deltotaria is considered sister to *Sigmoria,* partly from overall geography and partly from geographic congruence in general gonopodal form between members of each genus. We are aware of no autapomorphy for *Sigmoria* or for *Sigmoria + Deltotaria. Apheloria, Brachoria, Deltotaria,* and *Sigmoria* are partly sympatric, overlying mosaics. If each is viewed as having geographic properties of a species and thus originally allopatric, *Apheloria* may be considered northern, *Brachoria* western, *Deltotaria* southern, and *Sigmoria* eastern. Aside from congruence in gonopodal features, *Deltotaria* fits best with *Sigmoria* geographically.

The Tribal Hypothesis. — The following character statements document the tribal hypothesis in figure 161, eastern Xystodesmidae = Rhysodesmini + (Nannariini + (Pachydesmini + Apheloriini)).

6. *Retention or loss of a sternal remnant between the gonopodal coxae.* Gonopods are specialized ambulatory appendages, primitively joined by a sclerotized sternum. Retention of a sternal remnant is one of the characteristics of the Rhysodesmini (Hoffman 1960). Sclerotization is replaced by membrane in the other three tribes, an autapomorphous condition.

7. *Condition of pregonopodal tarsal claws in males.* The Nannariini is characterized by apomorphous twisted, spatulate, pregonopodal tarsal claws in males. In other genera the claws are bisinuately curved or uncinate, the plesiomorphic condition.

8. *Presence or absence of lateral subcoxal spines on postgonopodal sterna of males and midbody sterna of females.* These spines or lobes are found in the Nannariini and most rhysodesmine genera. In the Pachydesmini and Apheloriini, the caudal sternal edge is straight except for segments 8-10 where bicruciform grooves create a lobed appearance in some species. Absence of subcoxal spines or lobes is tentatively considered to be apomorphous.

9. *Body size.* The Nannariini and many of the eastern Rhysodesmini tend to be relatively small, whereas most species of Pachydesmini and Apheloriini are large *(Dicellarius okefenokensis, Sigmoria sigirioides,* and
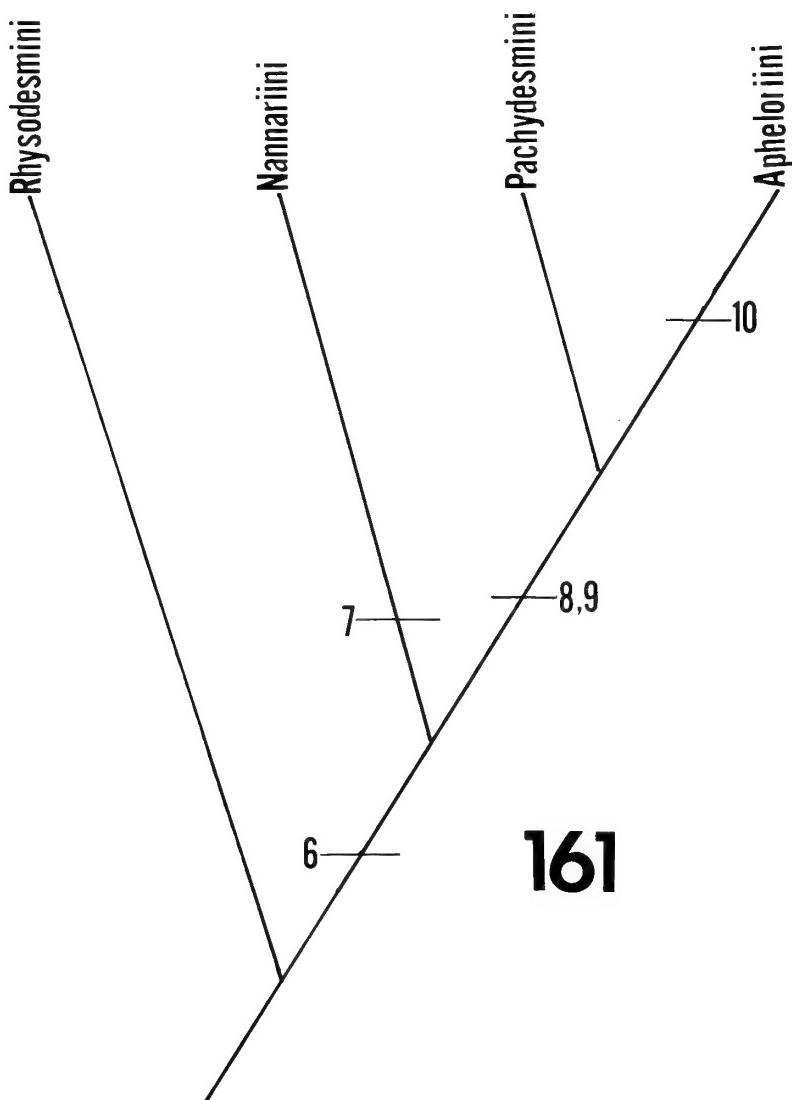
FIG. 161. Relationships among the four major xystodesmid tribes in eastern North America. The numbers refer to apomorphies discussed in the text.

S. truncata being exceptionally small). Large body size thus appears to be apomorphous and in combination with characters 7 and 8 joins the tribes Pachydesmini and Apheloriini as a monophyletic group.

10. *Condition of the prefemoral process.* Except for occasional individuals of the pachydesmine species *Dicellarius okefenokensis,* the prefemoral process is long, slender, and acicular in the Rhysodesmini, Nannariini, and Pachydesmini and therefore is considered plesiomorphous. In the Apheloriini, it is present or absent, but never acicular.

If monophyly in the Apheloriini is based on nonacicular prefemoral processes, we lack an autapomorphy for the Pachydesmini. Other known structural distinctions between the Pachydesmini and Apheloriini all involve exceptions, and tribal distinction may be unwarranted. Placement of *Dicellarius* and *Thrinaxoria* in the Pachydesmini by Shelley (1984c) was based on the similarity in character 10. The acropodite is divided in the Pachydesmini and undivided in the Apheloriini except in *Dynoria* and *Furcillaria*. All pachydesmines except *D. okefenokensis* lack acropodal torsion, and all apheloriines except *Dynoria* have it. Likewise, the acropodite is linear in all pachydesmines except *D. okefenokensis,* and curved or "sigmoid" in all apheloriines except *Dynoria* (secondarily curvilinear in the *planca* group of *Sigmoria).* Among genera of the Pachydesmini, *Pachydesmus* has coxal apophyses (convergent with those of *Deltotaria* in the Apheloriini) and large postgonopodal sternal elevations or podosterna (Hoffman 1958b), both conditions being autapomorphous. *Dicellarius* and *Thrinaxoria* have reduced cyphopodal receptacles, also autapomorphous. We have found no autapomorphous feature for all three genera, and this plus the exceptions regarding divided acropodites and torsion suggest that the two tribes should be combined. However, colors and color patterns may be as useful for characterizing tribes as they are for species within *Sigmoria,* but we have insufficient out-group information to assess polarity. The basic color pattern in the Apheloriini is a black body with bold paranotal spots and metatergal stripes. In contrast, the color pattern is generally pale among the Pachydesmini. Perhaps this lack of pigmentation in the Pachydesmini represents the missing autapomorphy.

Discussion. — These are not character rich hypotheses for either tribal or generic relationships. Other traits, such as facial chaetotaxy and meristic characters of the head and body, have not been analyzed sufficiently for interpolation.

Our comments on *Sigmoria* as a cohesive generic mosaic with a geographic structure virtually that of a single species led to speculation that the genus might be recent. It follows that much of the eastern xystodesmid fauna also may be recent. The endemic tribes Nannariini, Pachydesmini,

and Apheloriini, respectively with 2, 3, and 6 genera, form a monophyletic group. The putative sister group, Rhysodesmini, is presumed monophyletic, but we think it probably is not. Points of interest are these:

1. There is very little somatic differentiation among the endemic tribes. Distinctions between them and their genera and species are primarily gonopodal. Occasionally, species with very different gonopods are linked by intermediates (as in the *Sigmoria mimetica* group, for instance), so that gonopodal differences may be less significant than thought. Lack of somatic differentiation is consistent with suggested lack of age.

2. Failure to generate satisfactory cladistic hypotheses at the generic and tribal levels implies lack of extinctions needed to create structural gaps for definitions of lineages. Lineages are ill defined because of retention of ancestral features. Lack of profound structural gaps also is consistent with suggested lack of age.

3. We have reservations about the tribal classification proposed by Hoffman (1979), but the information at hand is insufficient to effect changes. Certainly, the distinction between the Pachydesmini and the Apheloriini does not appear to withstand scrutiny, and we do not think the picture among the entire eastern xystodesmid fauna is yet clear enough to determine where tribal limits should be set. Again, the absence of intensive analyses of *Apheloria* and *Brachoria* is a major gap in our knowledge, but comprehensive study is also needed in the Rhysodesmini. This tribe is both somatically and gonopodally diverse, and may need division. Neither Hoffman (1978c) nor Shelley (1980b) could adequately relate *Caralinda* to other rhysodesmines, and two recently discovered, small-bodied southeastern genera, *Parvulodesmus* and *Gonoessa* (Shelley 1983b, 1984d), are unique in having extremely long acropodites that overlap two or more segments *in situ*. We cite large body size as apomorphous for Apheloriini plus Pachydesmini, but small body size applies to the Nannariini and an increasing number of Rhysodesmini even though the largest xystodesmid of all, *Rhysodesmus dasypus* (Gervais), in Veracruz, Mexico, belongs to this tribe. Perhaps some of the eastern North American rhysodesmines combine with the other eastern tribes to form a monophyletic group. We can only speculate on this, but it becomes increasingly doubtful that all of the eastern rhysodesmine genera are contribal with *Rhysodesmus* and *Stenodesmus* in Mexico and Central America.

4. In conclusion, we again emphasize the importance of color, of which two basic patterns are displayed by the eastern xystodesmid fauna. In the Apheloriini and the Rhysodesmini (except for *Gyalostethus* and *Gonoessa,* which are comparatively dull; the color is unknown for *Parvulodesmus* and most species of *Caralinda)* the body is generally black and boldly marked by

stripes or spots. In the Pachydesmini and Nannariini, body color is neither black nor boldly marked. Instead, it is brown to olive to reddish orange, with or without paler stripes. We have no phyletic interpretation; bold patterns may be mimetic and therefore convergent in the Rhysodesmini and Apheloriini, as appears to be true for certain species of the latter. However, the basic color patterns do apply at the tribal level, and coloration in xystodesmids is far more interesting and informative than is generally recognized. It should become a standard and integral part of future systematic studies in the family.

LITERATURE CITED

ATTEMS, CARL G. 1931. Die Familie Leptodesmidae und andere Polydesmiden. Zoologica, Stuttgart, *30*:1-149.

—————. 1938. Polydesmoidea II, Fams., Leptodesmidae, Platyrhacidae, Oxydesmidae, Gomphodesmidae. Das Tierreich, Lief., *69*:1-487.

BOLLMAN, CHARLES H. 1888. Notes upon some myriapods belonging to the U.S. National Museum. Proc. U.S. Natl. Mus., *11*: 343-350.

CAUSEY, NELL B. 1942. Six new diplopods of the family Xystodesmidae. Ent. News, *53:* 165-170.

—————. 1950a. A collection of xystodesmid millipeds from Kentucky and Tennessee. Ent. News, *61*:5-8.

—————. 1950b. Two new polydesmoid diplopods. Ent. News, *61*:37-39.

—————. 1955. New records and descriptions of polydesmoid millipeds (Order Polydesmida) from the eastern United States. Proc. Biol. Soc. Wash., *68*:21-30.

CHAMBERLIN, RALPH V. 1918a. Myriapods from Nashville, Tennessee. Psyche, *25*:23-30.

—————. 1918b. New polydesmoid diplopods from Tennessee and Mississippi. Psyche, *25*:122-127.

—————. 1921. On some chilopods and diplopods from Knox Co., Tennessee. Can. Ent., *53*:230-233.

—————. 1939. On some diplopods of the Family Fontariidae. Bull. Univ. Utah. *30(2)*[Biol. Ser., *5(3)*]:1-19.

—————. 1943a. Some records and descriptions of American diplopods. Proc. Biol. Soc. Wash., *56*:143-152.

—————. 1943b. On some genera and species of American millipeds. Bull. Univ. Utah, *34(6)*[Biol. Ser., *8(2)*]:1-20.

—————. 1947. Some records and descriptions of diplopods chiefly in the collection of the Academy. Proc. Acad. Nat. Sci. Phila, *99*:21-58.

—————. 1949. Some millipeds of the families Polydesmidae and Xystodesmidae. J. Wash. Acad. Sci., *39*:94-102.

————— AND RICHARD L. HOFFMAN. 1958. Checklist of the millipeds of North America. Bull. No. 212, U.S. Natl. Mus., 236 pp.

FILKA, MARIANNE E. AND ROWLAND M. SHELLEY. 1980. The milliped fauna of the Kings Mountain Region of North Carolina (Arthropoda: Diplopoda). Brimleyana, *4*:1-42.

GRAY, JOHN E. 1832. Myriapods, *in* Griffith, The animal kingdom arranged in conformity with its organization by the Baron Cuvier, *15* (Class Insecta, 2):787.

HOFFMAN, RICHARD L. 1948. Two new genera of xystodesmid millipeds from eastern United States. Proc. Biol. Soc. Wash., *61*:93-96.

_____. 1949. Nine new xystodesmid millipeds from Virginia and West Virginia, with records of established species. Proc. U.S. Natl. Mus., *99*:371-389.

_____. 1950. American polydesmoid millipeds of the genus *Sigmoria,* with notes on distribution. Amer. Mus. Nov. No. 1462, 7 pp.

_____. 1951. Subspecies of the milliped *Apheloria trimaculata* (Wood) (Polydesmida: Xystodesmidae). Chicago Acad. Sci. Nat. Hist. Misc. No. 81, 6 pp.

_____. 1956a. Revision of the milliped genus *Dixioria* (Polydesmida: Xystodesmidae). Proc. U.S. Natl. Mus., *106*:1-19.

_____.1956b. Studies on some oriental xystodesmine millipeds. Proc. Ent. Soc. Wash., *58*:95-104.

_____.1958a. A new milliped of the genus *Sigmoria* from western North Carolina (Polydesmida: Xystodesmidae). Proc. Ent. Soc. Wash., *60*:281-284.

_____. 1958b. Revision of the milliped genus *Pachydesmus* (Polydesmida: Xystodesmidae). Proc. U.S. Natl. Mus., *108*:181-218.

_____. 1960. Revision of the milliped genus *Cherokia* (Polydesmida: Xystodesmidae). Proc. U.S. Natl. Mus., *112*:227-264.

_____. 1961. Revision of the milliped genus *Deltotaria* (Polydesmida: Xystodesmidae). Proc. U.S. Natl. Mus., *113*:15-35.

_____. 1962. A new genus and species in the diplopod family Xystodesmidae (Polydesmida). Proc. Biol. Soc. Wash., *75*:181-188.

_____. 1964. The status of *Fontaria pulchella* Bollman, with the proposal of a new genus and tribe in the diplopod family Xystodesmidae. Proc. Biol. Soc. Wash., *77*:25-34.

_____. 1966. The Mexican genera of Xystodesmidae (Diplopoda: Polydesmida). Trans. Amer. Ent. Soc., *92*:1-16.

_____. 1967. Revision of the milliped genus *Cleptoria* (Polydesmida: Xystodesmidae). Proc. U.S. Natl. Mus., *124*:1-27.

_____. 1969. The origins and affinities of the southern Appalachian diplopod fauna. pp. 221-246, *In:* Perry C. Holt, ed., 1969. The Distributional History of the Biota of the Southern Appalachians, Part I: Invertebrates. Research Division Monograph I, Virginia Polytechnic Institute, Blacksburg, VA, 295 pp + i-vi.

_____. 1970. Random studies on *Rhysodesmus.* I. Notes and redescriptions of miscellaneous species. Radford Rev., *24:*143-162.

_____. 1971. Millipeds of the genus *Brachoria* in Virginia (Polydesmida: Xystodesmidae). Radford Rev., *25:*83-99.

_____. 1978a. Revalidation of the generic name *Rudiloria* Causey, 1955 (Polydesmida: Xystodesmidae). Myriapodologica, *1(1)*:1-6.

_____. 1978b. Chelodesmid studies. XI. A new genus and species from Venezuela referrable to the new tribe Chondrodesmini. Rev. Suisse Zool., *85:*543-551.

_____. 1978c. A new genus and species of rhysodesmine milliped from southern Georgia (Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *91:*365-373.

_____. 1979. *Classification of the Diplopoda.* Museum d'Histoire Naturelle, Geneva, Switzerland, 237 pp.

HUNT, CHARLES B. 1967. *Physiography of the United States.* W.H. Freeman Co., San Francisco, 480 pp.

JACOT, ARTHUR P. 1938. Four new arthropods from New England. Amer. Midl. Nat., *20:*571-574.

JEEKEL, C.A.W. 1971. Nomenclator generum et familiarum Diplopodorum: A list of the genus and family group names in the class Diplopoda from the 10th edition of Linnaeus, 1758, to the end 1957. Monog. Nederl. Entom. Vereng. No. 5, 412 pp.

KEETON, WILLIAM T. 1959. A revision of the milliped genus *Brachoria* (Polydesmida: Xystodesmidae). Proc. U.S. Natl. Mus., *109:*1-58.

_____. 1960. A new genus and species of xystodesmid milliped from Tennessee. Bull. Brooklyn Ent. Soc., *55:*42-45.

_____. 1965. Descriptions of three new species of *Brachoria,* with notes on established species (Diplopoda, Polydesmida, Xystodesmidae). Proc. Biol. Soc. Wash., *78:*225-240.

KENYON, FREDERICK C. 1893. A preliminary list of the Myriapoda of Nebraska with descriptions of new species. Publ. Nebraska Acad. Sci., *3:*14-18.

KEVAN, D.K. McK. 1983. A preliminary survey of known and potentially Canadian millipedes (Diplopoda). Can. J. Zool., *61:*2956-2975.

LOOMIS, HAROLD F. 1943. New cave and epigean millipedes of the United States, with notes on some established species. Bull. Mus. Comp. Zool., *92:*373-410.

_____. 1944. Millipeds principally collected by professor V.E. Shelford in the eastern and southeastern states. Psyche, *51:*166-177.

SHEAR, WILLIAM A. 1972. A new milliped in the genus *Apheloria* from southern West Virginia, and the taxonomic position of *Rudiloria mohicana* (Diplopoda: Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *85:*493-498.

SHELLEY, ROWLAND M. 1976. Millipeds of the *Sigmoria latior* complex (Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *89:*17-38.

_____. 1977. The milliped genus *Croatania* (Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *90:*302-325.

_____. 1979a. A new milliped of the genus *Caralinda* from north Florida (Polydesmida: Xystodesmidae). Fla. Ent., *62:*183-187.

_____. 1979b. The status of *Sigmoria gracilipes* Chamberlin, with remarks on the milliped genus *Brachoria* (Polydesmida: Xystodesmidae). Fla. Ent., *62:*220-223.

_____. 1980a. The status of *Cleptoria shelfordi* Loomis, with the proposal of a new genus in the milliped family Xystodesmidae (Polydesmida). Brimleyana, *3:*31-42.

_____. 1980b. Revision of the milliped genus *Pleuroloma* (Polydesmida: Xystodesmidae). Can. J. Zool., *58:*129-168.

_____. 1981a. Revision of the milliped genus *Sigmoria* (Polydesmida: Xystodesmidae). Mem. Amer. Entomol. Soc. No. 33, 140 pp.

_____. 1981b. A new milliped of the genus *Brevigonus* from South Carolina, with comments on the genus and *B. shelfordi* (Loomis) (Polydesmida: Xystodesmidae). Brimleyana, *6:*51-60.

_____. 1981c. A new xystodesmid milliped genus and three new species from piedmont South Carolina (Polydesmida). Proc. Biol. Soc. Wash., *94:*949-967.

_____. 1982. A new xystodesmid milliped genus and three new species from the eastern Blue Ridge Mountains of North Carolina (Polydesmida). Proc. Biol. Soc. Wash., *95:*458-477.

_____. 1983a. The status of *Cleptoria divergens* (Chamberlin) (Polydesmida: Xystodesmidae). Myriapodologica, *1(12):*81-89.

_____. 1983b. *Parvulodesmus prolixogonus,* a new genus and species of xystodesmid milliped from South Carolina (Polydesmida). Proc. Biol. Soc. Wash., *96:*121-126.

_____. 1984a. Revision of the milliped genus *Cheiropus* (Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *97:*263-284.

_____. 1984b. Revision of the milliped genus *Dynoria* (Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *97:*90-102.

_____. 1984c. A revision of the milliped genus *Dicellarius,* with a revalidation of the genus *Thrinaxoria* (Polydesmida: Xystodesmidae). Proc. Biol. Soc. Wash., *97:*473-512.

_____. 1984d. A new xystodesmid milliped genus and five new species from the Coastal Plain of Alabama (Polydesmida). Fla. Ent., *67:*453-464.

WHITEHEAD, DONALD R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). Quaest. Entomol., *8:*131-348.

WILLIAMS, STEPHEN R. AND ROBERT A. HEFNER. 1928. The millipedes and centipedes of Ohio. Bull. Ohio Biol. Surv. No. 18, *4(3)/*[Ohio State Univ. Bull., *33(7)*]:93-146.

WOOD., HORATIO C. 1864. Descriptions of new species of North American Polydesmidae. Proc. Acad. Nat. Sci. Phila., *16:*6-10.

_____. 1865. The Myriapoda of North America. Trans. Amer. Philosoph. Soc., *13:*137-248.

WRAY, DAVID L. 1950. *Insects of North Carolina, Second Supplement.* NC Dept. Agric. Raleigh, 181 pp.

_____. 1967. *Insects of North Carolina, Third Supplement.* NC Dept. Agric., Raleigh, 181 pp.

Index to Taxa

Synonyms in *italics*, new species in **boldface**

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